PALEONTOLOGY

BY

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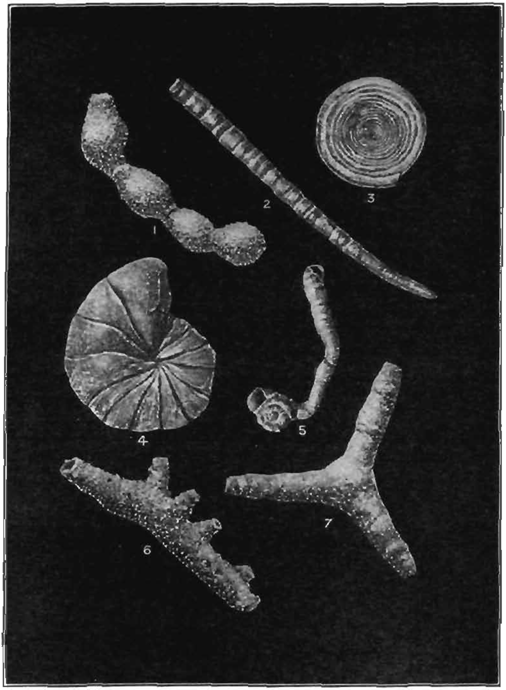

Frontispiece

Much enlarged views of several arenaceous Foraminifera, representing six of the families. 1. *Hormosina carpenteri* Brady. 2. *Bathysiphon rufum* de Folin. 3. *Ammodiscus incertus* d'Orbigny. 4. *Cyclammina cancellata* Brady. 5. *Trochammina lituiformis* Brady. 6. *Astrorhiza arenaria* Norman. 7. *Rhabdammina abyss*[illegible]

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TO

M. W. B.

PREFACE

Most elementary texts discuss fossils in their often fragmentary condition as traces of long-dead organisms dug out of the rocks and chiefly useful as indicators of geological horizons. It has always seemed to the author that fossils were quite as wonderful as anything in human experience—not, however, as dead fragments, or medals of creation, but as once-live organisms. The beginner is not interested in such philosophical questions as What is a species? nor can he be expected to identify fossil species precisely because this requires not only much experience but also reference collections and much literature. But he is interested in the drama of life as time and evolution have unfolded it, in the way in which the various organisms of the past played their part in the teeming world of long ago.

The chief emphasis in the present book is laid on two aspects of the subject: first, resemblances rather than differences, which is only another way of saying that the treatment is, as far as possible, evolutionary; and, second, adaptations of organisms to their environment. Without deviating from the facts, the purpose is to interest rather than to repel the beginner—a pedagogical principle all too frequently ignored.

The danger is always to say too much rather than too little in connection with each group, and in most groups the author, perhaps, gives more than necessary, believing that such a treatment might furnish suggestions to the instructor, who can omit those parts that may seem too technical. The work gives more space to the important groups, which are well represented by fossils, and whose relationships are more precisely known, and entirely omits certain groups of uncertain affinities or groups imperfectly known—a knowledge of which can readily be obtained from more advanced texts. In all cases, the student should be given the opportunity of seeing and handling actual specimens representing the principal groups discussed.

The text is simplified by numerous illustrations the majority of which are original, although the works of many authors have

been drawn upon, as indicated in connection with each. Wherever possible, these illustrations are somewhat diagrammatic for the sake of clearness, and those who use this work should study these figures, since none has been used as mere embellishment, but all are an integral part of the text.

E. W. B.

BALTIMORE, MD.,
April, 1929.

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PALEONTOLOGY

CHAPTER I

INTRODUCTION

It requires considerable experience in actually studying rock masses and geological processes to get a true appreciation of the length of geological time. The earlier geologists, starting with the then current theological conceptions of an earth only a few thousand years old, quite naturally imagined gigantic convulsions of nature to explain the folding of rocks, the rearing of mountains, or the flooding of land surfaces. The correct explanation, that small forces acting over immense stretches of time are more effective than mighty forces exerted suddenly, is an essentially modern view, and we now know that geological processes in the past were the same and moved at about the same rates as they do at the present time.

There are a great variety of methods for estimating the age of the earth, all containing unknown factors, so that none can be considered as conclusive. Among these methods may be mentioned the marvelous panorama of evolution as shown by the fossil record. We do not know the rate of evolution, nor was it uniform in different groups or in the same group at different times, so that all that comes of this method is a tremendous realization that vast lapses of time were involved. A favorite method of estimating time is that which computes the total thickness of sedimentary rocks all over the world and endeavors to get at the time by the known rate of accumulation of limestones, sands, or muds at present. These rates now, and throughout the past, are so dependent on the supply of material, the height of the land that was furnishing it, the amount of rainfall that was carrying it, that the method can never give precise results.

A third method rests on calculations of the present salinity of the oceans and the rate at which the rivers of the world are

carrying the various salts into the oceans, assuming that these were fresh at the beginning. The method is faulty, since it ignores the size of the land areas exposed to weathering, the kinds of rocks so exposed, the wetness or dryness of the climate, the enormous amounts not in solution but withdrawn from circulation, as rock salt, gypsum, and other salt deposits, and various other factors.

Another method, the latest and most fashionable, rests on the rate of disintegration of radioactive minerals. Using the observed rates, the age of such minerals in pre-Cambrian, Devonian, Cretaceous, or Eocene igneous rocks can be calculated. The results of this last method are impressive, and many geologists believe them to be very accurate, but it ignores the fact that the minerals used may themselves be the decomposition products of earlier radioactive minerals whose rates of disintegration we cannot hope to know. The fate of an earlier and seemingly conclusive method of determining the age of the earth, by the world's most eminent physicists and based on the rate of cooling of the earth's crust, should make us cautious.

Paleontology cannot be understood without some sort of time table any more than human history could be understood without dates or business be transacted without calendars or clocks. The geologic clock or time table is naturally somewhat of a patchwork, due to its having been built up as geological observations accumulated and became understood. An historical study of the origin of our present names would be highly interesting but would take us too far afield. We may, first of all, divide all geologic time into the five great eras: Archaeozoic, Proterozoic, Paleozoic, Mesozoic, and Cenozoic. The first two of these we may ignore, since their rocks have not as yet furnished anything but vague or circumstantial traces of organisms.

The remaining three comprise the well-known fossiliferous series of rocks containing ancient life (Paleozoic), intermediate or middle life (Mesozoic), and modern life (Cenozoic). Each of these eras is divided into periods of time, and each of these periods of time corresponds to what the geologists call a "system of rocks." The names of these systems and periods are of varied origin. Thus, in the Paleozoic era, the name Cambrian is derived from Cambria, the Roman name of Wales, where the rocks of that age were first studied. Ordovician and Silurian are derived from the names of native tribes in Britain formerly

inhabiting the areas where rocks of these ages were first studied. Devonian is derived from Devonshire; Carboniferous, from the abundance of coal (carbon) in its rocks; Permian, from the province of Perm in Russia.

The Mesozoic periods are Triassic, Jurassic, and Cretaceous. Triassic got its name from the threefold subdivision of its rocks in southern Germany, where they were first studied. Jurassic is named from the Jura Mountains; and Cretaceous, from the abundance of chalk (Latin *creta*) at the time. The Cenozoic periods are but two—Tertiary and Quaternary—and the second will eventually be discarded. Both indicate relative lateness and were proposed when geologists divided all rocks into Primary, Secondary, Tertiary, and Quaternary. The Primary now corresponds to Paleozoic and older; the Secondary, to Mesozoic; and only the Tertiary and Quaternary survive in our formal scheme.

Each of the periods of time is divided into what are called "epochs," but this and the still more minute divisions of geological time are best not considered until after the student has bad some geological experience. It is known that the Mesozoic era was about three times longer than the Cenozoic and that the Paleozoic was about three times as long as the Mesozoic or nearly ten times longer than the Cenozoic. The actual number of years is uncertain, but the whole certainly amounted to considerably more than a hundred million and probably was seven or eigbt times that figure.

The following abridged scheme will be sufficient for the purposes of this book:

Geological Time Table

Eras	Periods	Epochs	Outstanding features
Cenozoic (era of mammals and flowering plants) . .	Quaternary	Recent	Rise of civilizations
		Pleistocene	Glacial times
	Tertiary	Pliocene	Origin of man
		Miocene	Culmination of mammals
		Oligocene	Modern mammals, nummulites, and orbitoids
		Eocene	Archaic mammals

Geological Time Table.—(*Continued*)

Eras	Periods	Epochs	Outstanding features
Mesozoic (era of dinosaurs, ammonites, and cycads)..	Upper Cretaceous		Specialization of dinosaurs, extinction of ammonites
	Lower Cretaceous		Rise of flowering plants
	Jurassic		Toothed birds and flying reptiles
	Triassic		Ammonites and dinosaurs, first mammals, last Orthoceras
Paleozoic (era of invertebrates, fishes, and ancient plants)...........	Permian		Rise of land vertebrates
	Upper Carboniferous		Coal plants, primitive reptiles, insects
	Lower Carboniferous		Amphibians, sharks, and crinoids
	Devonian		Corals, rise of Goniatites, oldest known land plants
	Silurian		Armored fishes
	Ordovician		Rise of cephalopods, age of graptolites
	Cambrian		Trilobites and brachiopods
Pre-Paleozoic or pre-Cambrian..........			Very great thickness of rocks representing about half of geologic time and with scarcely *any fossils.*

CLASSIFICATION

The student is apt to believe that the learning of a given classification is something important and is inclined to be dismayed when he subsequently finds wide diversities of presentation in different texts based upon the same body of facts. It is much more important for the beginner to acquire a good idea of the characteristic features of each of the great groups of animals so that he will know at once that a given specimen is a coral or a hryozoan, a brachiopod or a mollusk, a fish or an amphibian. Classifications of organisms may be compared to filing systems or to the arrangement of books in a library. Opinions will always differ as to the most logical arrangement, and there is a real difficulty in the case of those organisms which fit in one pigeon hole about as well as in another. The very nature of evolution presupposes the absence of sharp boundaries, and the more we learn of the history of organisms the more difficult it

becomes to maintain such boundaries. It is the same in using fossils for the determination of the age of rocks—the boundaries of the geological time table are more or less artificial. Any competent paleontologist will readily distinguish between a typical Devonian and a typical Carboniferous fauna or between a typical Jurassic and a typical Cretaceous one, but it is not easy to discriminate between a late Devonian and an early Carboniferous or a late Jurassic and an early Cretaceous one, and of course the one really passes into the other as imperceptibly as one passes from boyhood into manhood, and our time boundaries are quite as arbitrary as that of the common law according to which, in legal phraseology, a boy passes from infancy to manhood at the age of twenty-one years.

At the beginning of our introduction to paleontology we do need to get a bird's-eye view of the whole animal kingdom—not formal definitions of the features of this, that, or the other group—but a general appreciation of the respective grades of organization of each of the great groups and of their relations to one another. First, animals may be separated into two grand divisions according as their bodies consist of a single cell or many cells. The single-celled animals are the Protozoa, and the many-celled are the Metazoa. The term Protozoa finds a place in the scheme of classification as the name of the simplest known animal phylum. The Metazoa comprise all the rest, including the more familiar animals, and the name does not find a formal place in classifications because it embraces such a diversity of unrelated forms.

Among these diversified Metazoa or many-celled animals, we at once distinguish between those in which the cells are but partially specialized and compacted into tissues or organs—the Porifera or sponges—and all of the remainder in which cell specialization (nerve, muscle, blood, etc.) results in definite systems of tissues. Among the latter we find that one large group has but two body layers—an inner or endoderm and an outer or ectoderm. This is the phylum Cœlenterata which includes such familiar things as corals, sea anemones, and jellyfishes. The plan of the body is that of a sac whose interior is known as the "gastrovascular cavity" or "cœlenteron," because its walls serve all the functions of digestion, secretion, circulation, and frequently reproduction. Contrasted with the Cœlenterata, all of the remaining animals have three body layers—an inner

or endoderm, a middle or mesoderm, and an outer or ectoderm. Thus far, our progress has been simple and easily understood, and a cardinal feature of the three subkingdoms Protozoa, Porifera, and Cœlenterata has been given. The remaining animals are less simple. First of all, in considering those animals with the three-body layers endoderm, mesoderm, and ectoderm, we note that in the so-called "lower" worms, which, for simplicity's sake will not be named, since they are not preserved as fossils, the mesoderm is solid. That is, it does not split during development to form a body cavity, known as a cœlome (from the Greek *koilos*, meaning "hollow"), which is present in the higher worms and all the remainder of the animal kingdom. This furnishes a good illustration of why classifications differ. Some naturalists, seizing on the fact that all of the more advanced invertebrates not yet enumerated and that all of the vertebrates have a cœlome, would coin the term Cœlomata for them. Although we recognize the cardinal fact that they have such a body cavity and are cœlomatic, they are so diverse in other respects that we use the more familiar names for the phyla or subkingdoms and do not try to embalm all of our knowledge in the formal classification.

Now, among the worms which have a cœlome, some have their bodies divided into segments and some are unsegmented. The unsegmented forms are less modified descendents of ancestors very similar to the ancestors of the segmented worms as well as the ancestors of the subkingdoms Bryozoa, Brachiopoda, Echinoderma, Mollusca, and the simpler Chordata. The proof of this rests upon rather abstruse morphological and embryological facts, but a simple illustration will give a hint of the evidence. Among the myriad of modifications of form and habit in these phyla, in the case of all the kinds in which the eggs are laid in the water and there are no devices for parental care, the eggs hatch as free-swimming larvæ quite unlike their parents. Although differing in detail, these free-swimming larvæ are remarkably alike in their general form and structure. All have a simple, bent alimentary canal, a ring of cilia in front of the mouth, one or more flagella at the larger end, beneath which is a ganglion, and there may be additional rings of cilia, in some cases.

Such a free-swimming larva in the Mollusca is called a "trochosphere," and those in the other groups are so like a trochosphere in their organisation that many naturalists think that these give

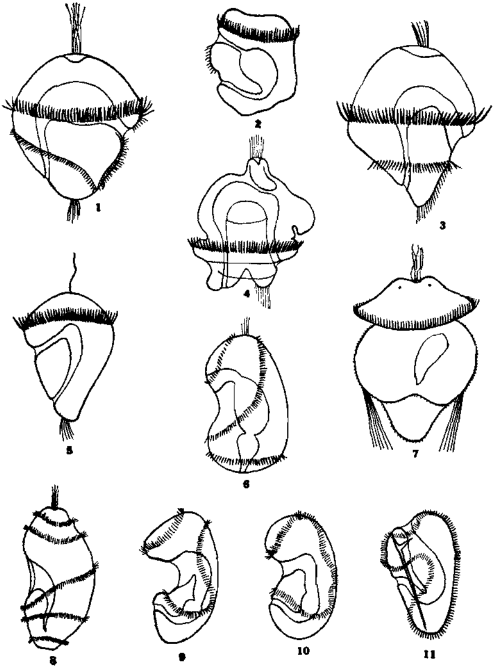


FIG. 1.—Much magnified free-swimming young of various invertebrate animals. 1. *Polygordius*, an annelid worm. 2. An oyster, Ostrea. 3. *Eupomatus*, one of the serpulid worms. (*After Hatschek.*) 4. Pedicellina, one of the Bryozoa. (*After Hatschek.*) 5. Dreissensia, a bivalved mollusk. 6. Tornaria of Balanoglossus. 7. A brachiopod, Megathyris. 8. A crinoid, Antedon. (*After Seeliger.*) 9. A sea star, Bipinnaria. 10. A sea cucumber or holothurian, Auricularia. 11. A sea urchin or echinoid, Pluteus.

us something of an idea of what the remote pelagic ancestors of these various groups were like in pre-Cambrian times. The entirely hypothetical group Trochozoa in the diagram on page 9 indicates such a possible relationship.

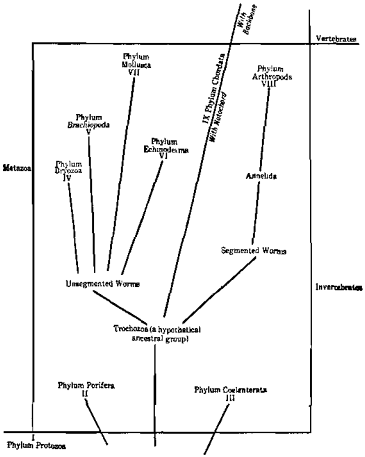
All of Fig. 1 show much magnified median sections of various trochosphere-like larvæ, and, as may be seen, their resemblance is very striking. Figure 1^{1} is that of a segmented worm (Polygordius); Fig. 1^{2} that of the common oyster; Fig. 1^{3} one of the tube-forming worms (Eupomatus); Fig. 1^{4} one of the Bryozoa (Pedicellina); Fig. 1^{5} a bivalved mollusk; and it will be noted that these first five, whose parents are so diverse at maturity, are so much alike as larvæ that it would take a very expert naturalist to tell which was which; Fig. 1^{6} shows what is known as a "tornaria larva" of a form (Balanoglossus) that belongs near the base of the Chordata line of evolution.

Figure 1^{7} is that of a brachiopod, which differs from the others merely in its lobation and in the fact that the future alimentary tract has not yet reached the surface to form the mouth and anus. Figures 1^{8}, 1^{9}, 1^{10}, and 1^{11} represent the larvæ of various echinoderms, Fig. 1^{8} being that of the crinoid genus Antedon; Fig. 1^{9} known as a "bipinnaria," that of a sea star; Fig. 1^{10}, known as an "auricularia," that of a holothurian; and Fig. 1^{11} a larva known as a "pluteus" which will mature as a sea urchin (echinoid).

The conclusion is, then, that both segmented and unsegmented worms originally had similar ancestors like the ancestral stocks that gave rise to the subkingdoms Bryozoa, Brachiopoda, Echinoderma, and Mollusca. This accounts for the origin of all of the animal subkingdoms except the Chordata, to which man himself belongs; and the Arthropoda—articulated animals such as insects, crustaceans, spiders, and their kin. It has been indicated that the Chordata probably have an origin similar to that of the preceding great groups. Among the more complex segmented worms, the group known as the Annelida gives the best picture of the probable ancestry of the subkingdom which includes insects, trilobites, spiders, etc., and which is known as the Arthropoda.

All of the subkingdoms mentioned, except the Chordata, have a fundamental point of resemblance in that they show no trace of a notochord—a cartilaginous axial rod which is the foreshadowing of the spinal cord of the vertebrates.

The Bryozoa, Brachiopoda, Echinoderma, and Mollusca have, through long ages, become adapted for their various stations in life. All are aquatic except the land snails, and all except a few Bryozoa and a few Mollusca have always been marine. The Bryozoa remain small and soon become attached and colonial. The Brachiopoda are larger, they attach themselves and secrete an upper and lower valved shell. The Echinoderma became diversified, passed through a period of attachment which impressed



on the adults a radial symmetry—a stage of their history represented by the existing sea lilies—several of their classes such as the sea stars, sea urchins, and sea cucumbers (holothurians) became free and developed a multiplicity of forms. The primitive arthropods are all marine, and among their early forms some became terrestrial and gave rise to the spiders, scorpions, and centipedes and, later, to the host of winged forms—the insects.

The simpler Chordata took two diverse paths of evolution, the one leading to a loss of the notochord that shows only in their

swimming larvæ, becoming attached or free floating and maturing as so-called "sea potatoes" and "salpas" (tunicates or ascidians).

The other line remained active, retained the notochord, and eventually perfected it as a vertebral column. From that point onward they were vertebrates and successively differentiated through the aquatic fishes to the amphibians and terrestrial reptiles, the birds, and the mammals. These relations may be summarized in the diagram on page 9 which is not a geneological tree but simply a plan of relationships showing gradations in organization.

Paleontology is the biology of the past. Its subject matter comprises the animals and plants which lived in all geological periods and were preserved as fossils, so that in a very true sense it may be considered as the zoology (paleozoology) and botany (paleobotany) of all that vast lapse of time, to be measured in tens or hundreds of millions of years, which preceded the present or Recent period. The present text treats of only the animal or paleozoological portion of this record.

In dealing with the remains of animals preserved as fossils we should expect to find them broken, crushed or dismembered, with generally only their hard parts preserved—shells, teeth or bones, so that we cannot verify the details of their coloration and anatomy as we can in recent animals, and can only infer their habits and habitats.

These drawbacks are nevertheless far outweighed by the fact that we deal with the actual records of the drama of life, the documents of evolution, and these show us hosts of long extinct forms, ancestral to or intermediate between or totally unlike existing animals.

CHAPTER II

THE PROTOZOA OR SINGLE-CELLED ANIMALS

The *Protozoa* constitute a world which was unknown to man before the invention of the microscope, although they are not all microscopic; and the first shells were not discovered until 1730. They are the most universal and omnipresent animals and in recent years have acquired a vital interest as the cause of certain human ills such as malaria, African sleeping sickness, amœbic dysentery, etc.

Their outstanding attribute is that the whole animal is but a single cell, corresponding to a single epithelial, muscle, nerve, or bone cell that makes up the tissues of all the rest of the animal kingdom, or *Metazoa.* Although the protozoon is morphologically a single cell, it performs most of the functions, such as assimilation, growth, excretion, and reproduction, of the multiple-celled or tissue-forming animals.

The Protozoa are elaborately classified in groups, of which the major are readily distinguished by the nature of the protoplasmic processes (pseudopodia) by which they move. One of the large and most specialized groups swims by the movement of cilia and is, hence, often called the Ciliata, or it may be termed the Infusoria, since the classic way to obtain them was to make an infusion of hay or meat and let it stand a few days in an open vessel. Another great group is called the Flagellata, since its members are provided with a single or a few long whiplike protuberances which they lash about in swimming. Neither of these groups has any hard parts; consequently, they are not represented in the geological record, although we have every reason to believe that they are very ancient.

A third great group is distinguished by having its processes intermittent and irregular and, hence, was christened the Rhizopoda (root footed). The members of this group may be formless specks of protoplasm like the amœba, and such are not fossilized. Others secrete a definite skeleton, and these are frequently found fossil. The latter represent two great groups of Rhizopoda known as the Radiolaria and the Foraminifera.

Foraminifera.—These are minute forms varying from a fraction of a millimeter to several millimeters and, more rarely, reaching a diameter of several centimeters. A few live in fresh or brackish water, but the vast majority are marine. They occur at all but are most frequent in moderate depths. In regions remote from land-derived sediments, their dead shells rain down on the ocean bottoms and form a characteristic calcareous ooze known as Globigerina or *Biloculina* ooze. Throughout the group there are series of gradations from those in which the surface of the protoplasm is simply stiffened but flexible, through forms in which the surface becomes horny (chitinous), like the fresh-water family Allogromidæ, and these will not occur as fossils. The next step in the direction of a more permanent covering is the use of chitin as a base or cement for holding together a rubble-like mass of sand grains. Such forms are readily preserved in the rocks. Gradually we pass to forms in which the cement is calcareous, and from these it is but a step for them to discard foreign material and build the whole shell of secreted calcium carbonate.

Although the protoplasmic body is a single cell, the shell may be a single or many chambers, and the general course of foraminiferal evolution seems to have been from single-chambered and irregular shells to many-chambered and symmetrical shells, often followed by an evolutionary reduction or simplification. Shells consisting of a single chamber are said to be unilocular (Latin) or monothalmous (Greek). Many-chambered shells are said to be multilocular (Latin) or polythalmous (Greek). Some authors prefer to use the Latin and others the Greek terms.

Each shell has one or more relatively large openings, known as apertures, and in the calcareous foraminifera the shells when magnified will appear opaque and chalky (porcelaneous) or more or less glassy (vitrocalcareous). Some have fine, radial canals in the walls which give the surface a punctate appearance when rather highly magnified. It is these punctations that suggested the name Foraminifera (Latin *foramina*, a "tiny opening") for the group, although many do not possess foramina, and they are obvious only in those forms in which they are largest, which are forms living near the surface of the ocean, such as Globigerina. Other groups show no traces of foramina, and formerly the calcareous forms were divided into two groups—Perforata and Imperforata, according as foramina were present or absent. It

is now believed that the presence or absence of foramina is an adaptive character dependent on pressure, constitution of the protoplasm, and similar factors. In some groups, the young have perforate shells, and the adults imperforate shells, thus suggesting that the perforate was the ancestral condition.

The vast majority of the Foraminifera most useful in paleontology are the calcareous forms, because their shells are much more regular than most of those that build a shell of cement and sand grains. The latter are more primitive than the calcareous forms and are generally known as "arenaceous" (from the Latin for "sandy").

The more ancient of these arenaceous forms have but a single chamber with one or more large apertures (Frontispiece, Figs. 6 and 7), or there may be several irregularly arranged chambers (Frontispiece, Fig. 5). The more advanced families, such as the Ammodiscidæ (Frontispiece, Fig. 3) or Lituolidæ (Frontispiece, Fig. 4), are regularly arranged and foreshadow the calcareous types, as do the representatives of the family Reophacidæ (Frontispiece, Fig. 1) and Rhizamminidæ (Frontispiece, Fig. 2).

Every calcareous species in which the shells have been studied shows two kinds of shells identical in appearance but with a different early development. These are known as "microspheric" when the initial chambers are small and "megaspheric" when the initial chambers are large; the former represents a sexual generation, and the latter an asexual one.

Origin of Shell Form.—From a study of Fig. 2, which represents diagrammatic sections of actual shells, the student may readily visualize the simple way in which a variety of shell forms may originate.

The young Foraminifera starts its shell by secreting a first single small chamber. This is known as a proloculum, and all "forams" are very similar in this proloculum stage, which is represented in solid black in the figure.

In Fig. 2^1 when the protoplasmic body has outgrown the capacity of the proloculum it will have overflowed from the neck of the flask-shaped chamber, and it then secretes the wall of a second chamber, repeating this process at intervals for each succeeding chamber in a straight or slightly curved series. The final result is the beautiful wandlike forms known as Nodosaria.

Or the first two chambers may be nodosarian, after which the protoplasmic material may increase so greatly that the third

chamber completely encloses the second, and the remainder may continue to be formed like the first two. Such a succession takes place in the forms known as Dimorphina (Fig. 2^{2}).

Figure 2^{3} illustrates a form—Polymorphina—in which the first three chambers are formed exactly as in Dimorphina, but

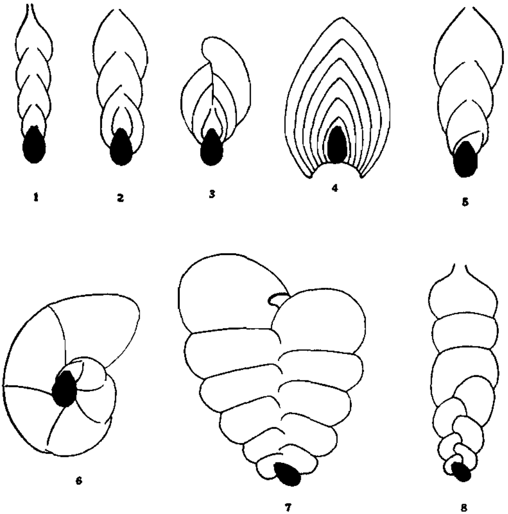


FIG. 2.—Showing types of shell architecture in the Foraminifera. A series with a Lagena-like proloculum (in solid black). Much magnified. 1. Nodosaria. 2. Dimorphina. 3. Polymorphina. 4. Frondicularia (megaspheric form). 5. Marginulina. 6. Cristellaria. 7. Textularia. 8. Bigenerina.

the later chambers fan out and have the upper part of the walls alternating. Figure 2^{4} develops successive chambers in a linear series, as in Nodosaria, but the overflow of protoplasm occurs only on opposite sides of the aperture and extends downward to the base or farther. Consequently, the whole is flat, and the lower part of each new chamber partially or wholly encloses the earlier chambers. This is the Frondicularia type of shell.

Figure 2^5, which represents a genus known as Marginulina, has the second chamber tilted and the remainder straight. Figure 2^6 is a very common type and results from the fact that each successive chamber is much tilted; that is, the new wall is much more developed on one side, giving a shell in which the chambers are coiled in a plane (planospiral), and is known as Cristellaria.

In Fig. 2^7, the new chambers are formed first on one side and then on the other, resulting in a double row of alternating chambers (biserial). This is the Textularia type of shell. Figure 2^8 shows the plan of a form known as Bigenerina, which, in its youth, is like Textularia but later adds new chambers in a single series, and it is inferred from this that it was descended from some textularian ancestor.

These diagrams will show how Foraminifera are studied, and include three of the principal types of shell architecture, namely:

1. Chambers straight or but slightly curved in a linear series: nodosarian.

2. Chambers in a linear coiled series forming an equilateral or symmetrical planospiral. Cristellaria was the example given, and this type of architecture might well be called cristellarian, but it happens to have been named "nautiloid" because it is similar to the arrangement of chambers in the pearly nautilus, a well-known and famous cephalopod mollusk, and the early students of "forams" thought that the Foraminifera were minute cephalopods.

3. A double row of alternating chambers: textularian.

There are two additional regular arrangements of chambers. These are:

4. Chambers in which the shell is coiled, but the coil is not in one plane, ascending instead like the shell of a snail. This style is called "trochoid" from its resemblance to Trochus—one of the marine snails.

5. This is somewhat difficult to visualize. Each succeeding chamber embraces part of the preceding chamber around an imaginary axis, and the type is known as "milioline." Each chamber may be 180 degrees from the preceding (Biloculina), or 120 degrees (Triloculina), or 72 degrees (Quinqueloculina). A Biloculina shell is shown in section in Fig. 3^2 which illustrates the plan of the megaspheric form. Figure 3^1 shows the microspheric form, which is seen to have passed through a Quinqueloculina stage in chambers 1 to 8 and a Triloculina stage in chambers 9 to

11, after which it also is a typical Biloculina. These early stages are absent in the megaspheric form of the species. A whorl is the distance once around the axis of a spiral form, and the lines of union between the walls of adjacent chambers as seen from the outside of the shell are called "sutures."

A few selected examples taken from some of the better known families will serve to illustrate the evolution of shell form in these groups.

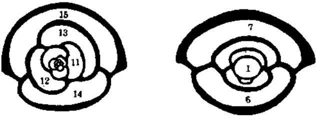


FIG. 3.—Median sections of a shell of Biloculina greatly enlarged. 1. Microspheric and 2. Megaspheric forms.

The family Peneroplidæ comprise calcareous forms in which the first or the first and second chambers are perforate and the later chambers imperforate. The aperture is a narrow ellipse in the more primitive members of the family, and this ellipse becomes broken up into a number of small openings in the more specialized forms—a modification increasing the mechanical strength of the shell, since numerous small openings impair the strength less than a single very large opening.

At least a dozen genera are recognized, some as ancient as the Cretaceous period, and all but five still living. All of these genera can be derived from a simple planospiral shell form, the modifications of such an ancestral type taking the form of uncoiling, or flattening and flaring, or becoming disklike with concentric rings of small chamberlets. In the present-day oceans, they are limited to shallow warm waters. In the accompanying figures, the ancestral spiral type of shell is shown by the youthful, more heavily shaded parts. This is most clear in Spirillina (Fig. 4^1), a Cretaceous to Recent genus, in which the later chambers are in a straight linear series, so that we may call this simple spiral part a "pre-Spirillina" stage. In the genus Peneroplis (Fig. 4^2), the chief difference is the great flare of the shell in the plane of the spiral and a flattening of the shell at right angles to it, resulting in a fanlike form. In the genus Orbiculina (Fig. 4^3), a Miocene

to Recent type, can be seen the pre-Spirillina stage, outside of which can be seen a Peneroplis-like stage, followed by rings of chamberlets. In Orbitolites (Fig. 4[4]), an Eocene genus, pre-Spirillina, Peneroplis, and Orbiculina stages can be made out, followed by a perfectly circular, disklike stage in which there are many rings of tiny chamberlets.

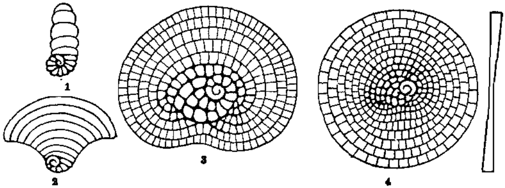


FIG. 4.—Evolution of the shell in the family Peneroplidæ, enlarged. 1. Spirillina. 2. Peneroplis. 3. Orbiculina. 4. Orbitolites.

In the familiar family Globigerinidæ, which includes more than half of the existing surface species of the oceans and whose dead shells form the globigerina ooze, all of the members may be derived from an ancestral form like Globigerina (Fig. 5[1]), a Cretaceous to Recent genus, in which a relatively few globular chambers are arranged in an imperfect spiral. The Tertiary

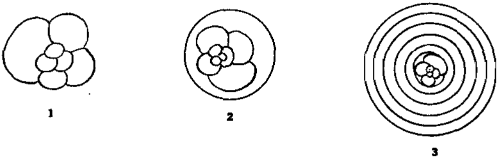


FIG. 5.—Evolution of the shell in the family Globigerinidæ, enlarged. 1. Globigerina. 2. Orbulina. 3. Cycloloculina.

to Recent genus Orbulina (Fig. 5[2]), often considered as consisting of a single spherical chamber, is not really so, but the young shell is like a Globigerina, and the last-formed chamber is a sphere completely enclosing all of the earlier chambers, and these are frequently resorbed (dissolved away). The spherical form is an almost perfect adaptation for a floating near surface organism, attained in the manner described in Orbulina and approximated

in the arrangement of the chambers in Globigerina. A curious modification of the Globigerina ancestral form is shown in the Eocene genus Cycloloculina (Fig. 5³) in which the young shell is exactly like a Globigerina, but in which each later chamber is a complete ring.

This annular modification shown in the Peneroplidæ and Globigerinidæ is evidently an adaptation, since it makes its appearance in so many unrelated lines of evolution among the Foraminifera, especially in those larger forms of the early Tertiary which have been found so important for indicating geological horizons. These larger Foraminifera belong to the two related families Nummulitidæ and Orbitoididæ. Their ancestry can be traced back to forms as ancient as Archædiscus of the Lower Carboniferous.

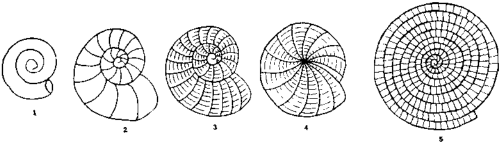


FIG. 6.—Stages in the specialization of shell form in the family Nummulitidæ, enlarged. 1. Archædiscus. 2. Operculina. 3. Heterostegina. 4. Polystomella. 5. Assilina.

In Archædiscus the spiral is not quite regular and consists of but two chambers—the initial chamber or proloculum and a long tubular, coiled, second chamber (Fig. 6¹). By Lower Cretaceous time this stock had assumed a shell form prophetic of its complex Tertiary descendants and may be illustrated by Operculina (Fig. 6²). Operculina had a shell which was lens shaped and consisted of three or four whorls of rapidly expanding chambers. A difference in the structure of the shell walls and partitions now becomes apparent. Each time the growth of the protoplasm causes an overflow and the formation of a new chamber the extruded protoplasm secretes a layer of calcareous material on its whole periphery. This results in the walls' being double where they are in contact and also causes the partitions to have double walls with tiny interspaces or canals left between the earlier- and later-formed parts (Fig. 7¹). This was the beginning of the so-called "canal system" so characteristic of the later and more complex types.

From this point onward, evolution proceeds in the direction of progressively increasing the number of the whorls, the subdivision of the chambers into chamberlets, and the overlapping of the shell walls toward the axis of the shell. The next step may be illustrated by Heterostegina (Fig. 6[3]), an Eocene to Recent genus, in which the whorls are slightly more numerous than in Operculina, and the simple chambers of Operculina are divided into a large number of chamberlets by tiny cross-partitions. A modification of the Heterostegina type is illustrated by Polystomella (Fig. 6[4]), a long-lived genus that ranges from the Jurassic to the Recent. The whorls in Polystomella are exactly

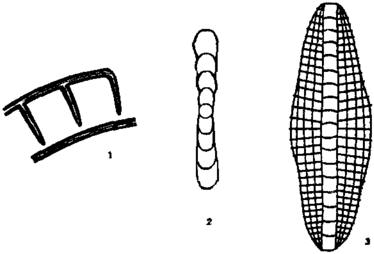


FIG. 7.—1. Greatly enlarged section of two chambers of Operculina, showing the double walls (black) and their enclosed canals (white). 2. Transverse section of Assilina showing the slight inward overlapping of the whorls. 3. Transverse section of Nummulites.

like those of Heterostegina, but the side walls of the shell overlap inward to the center (axis), so that from the outside all of the earlier whorls are hidden by the last-formed whorl.

The Eocene genus Assilina (Fig. 6[5]) is a form that is very close to Nummulites. The spiral is now a very low one with a large number of whorls and many chamberlets. Nummulites itself differs from Assilina chiefly in its cross-section. In Assilina the side walls of the shell overlap slightly, but there is but one series of chamberlets (Fig. 7[2]). Nummulites has, in addition to this equatorial series of chambers, several secondary whorls of chambers on each side, and radial strengthening pillars are formed (Fig. 7[3]). Nummulites is exceedingly abundant in Eurasia, forming massive limestones in the Alps, Himalayas, and other mountain chains. A species about the size of a coat button is

the chief constituent of the Egyptian limestone of which the pyramids of Gizeh were built. Some species of Nummulites are the largest known Protozoa, their shells reaching a diameter of neary 3 inches. Nummulites is rare in the Americas, its place being taken by the similar-looking members of the allied family Orbitoididæ.

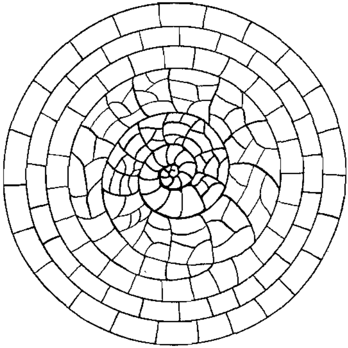


FIG. 8.—Cycloclypeus in median section showing an early Operculina stage, a second Heterostegina stage, and an adult orbitoid stage, much enlarged.

The outstanding difference between these two families is that in the Nummulitidæ the whorls are invariably spiral, whereas in the Orbitoididæ they are in concentric rings (cyclic). The transition from the spiral to the cyclic or annular arrangement, as we have seen it taking place in other families of Foraminifera, may be illustrated, in this case, by the genus Cycloclypeus (Fig. 8), which in its growth stages passes through an early Operculina stage and then a Heterostegina stage, the last two or three whorls passing gradually from the spiral to the concentric-ring arrangement. It requires but the subordination of the early stages and a very greatly increased number of rings to become a true orbitoid.

These true orbitoids all develop secondary rings of small chambers on both sides of the equatorial ring and strengthening pillars like those of Nummulites. There are many genera and species of Orbitoididæ during the earlier half of the Tertiary, and they are exceedingly abundant and often considerable rock

formers in equatorial America and in the southeastern Asiatic region. All look much alike superficially, and the chief and sometimes the only means of recognizing the genera is by grinding equatorial sections so that the earliest chambers and the geometric pattern of the chambers constituting this equatorial ring can be seen. These, especially the form of the earliest chambers, are quite diagnostic. Thus, in the Cretaceous genus Orbitoides the equatorial chambers are diamond shaped; in the Eocene genus Orthophragmina, or Discocyclina, as it is more properly called, they are elongated rectangles; in the chiefly Oligocene genus Lepidocyclina they are hexagonal; and in the Miocene genus Miogypsina they are rhomboidal.

A great many species of both recent and fossil Foraminifera have been recognized, and these are now arranged in about 40 families. They have been detected in rocks as old as the earlier Paleozoic but appear most abundantly in the Tertiary and Recent. Frequently, they have been abundant enough to form rocks of considerable extent even in the Paleozoic, such as the Lower Carboniferous limestones made up largely of the shells of the genus Endothyra. In the Upper Carboniferous all over the world are found what are known as Fusulina limestones made up of vast numbers of shells of the genus Fusulina and its allies, the shells of which have a size and form much like wheat seeds. Similarly, in the Eocene and Oligocene there are many nummulitic or orbitoid limestones.

RADIOLARIA

The second group of Protozoa which occur as fossils—the *Radiolaria*—are, for the most part, microscopic, and their smallness and the difficulties attending their identification are so great that they have been very little studied by paleontologists, although they have been recognized in rocks as old as the pre-Cambrian, and there are no more beautiful objects in all nature. Those Radiolaria which have hard parts have an inconceivably elaborate lattice-like skeleton of amorphous silica.

Radiolaria are exclusively marine at the present time, although a probable offshoot of the marine stock has become adapted to fresh water and constitutes the Heliozoa or "sun animalculæ," which are not found fossil. In the Carboniferous period, certain marine Radiolaria became adapted to the brackish or fresh waters of the coastal lagoons and coal swamps where the water

was highly charged with organic matter, in consequence of which their skeletons became horny and more flexible (family Traquairidæ).

The existing Radiolaria are all marine; the vast majority are pelagic—that is, they float passively in waters of the oceans, certain groups being characteristic of certain depths. Their indestructible skeletons gradually settle to the bottom, and in the greater oceanic depths where there are little or no land-derived sediments, they accumulate as almost pure deposits known as "radiolarian ooze." Such deposits cover large areas in depths greater than 10,000 feet—depths at which the calcareous shells of the Foraminifera are dissolved.

Fossil Radiolaria have been detected throughout the geological column from the pre-Cambrian to the present, but they are so small in size and so easily destroyed by subsequent solution that they are usually not detected in ordinary sediments except by painstaking search. In special kinds of rocks such as marine diatomaceous earth, cherts, flints, and certain marine limestones, they may be found in considerable abundance at any geological horizon where such rocks occur.

In order to understand the plan of the radiolarian skeleton, it is necessary to explain the main features of their protoplasmic structure. Their soft body is differentiated into an internal sphere (capsule) of tougher protoplasm in which the nucleus is embedded, and this sphere is bounded by a single or double membrane somewhat horny in character, outside of which there are one or more jelly-like layers, the inner of which is frequently colored (pigmented) and from the outer of which the slender radial pseudopodia are protruded.

If the membrane of the central sphere is uniformly perforated, the skeleton tends to be spherical and with a uniform surface pattern. If the perforations are clustered at one pole of the sphere, the resulting skeleton tends to assume a conical or helmet-shaped form.

CLASSIFICATION

The Radiolaria fall naturally into the following four classes, of which only two have skeletons permanent enough to become preserved as fossils:

1. **Class Peripylaria** (Spumellaria) from the Greek roots *peri*, "around," and *pyle*, "hole," in allusion to the uniform holes in

the single membrane of the capsule. The skeleton is of pure silica. *Figures* 9^2 and 9^6 *illustrate* this type.

2. **Class Acantharia** which afford no fossil forms. The name is in allusion to the supposition that the skeleton consisted of acanthin, a horny substance, although students are not agreed as to its chemical composition.

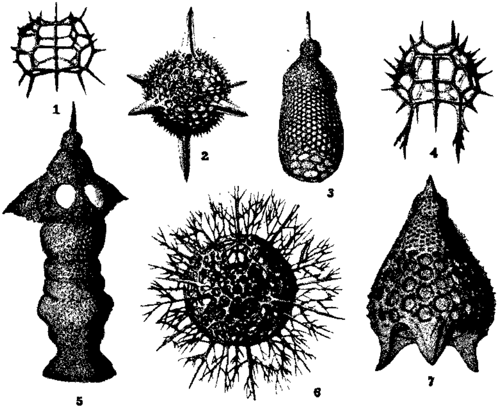


Fig. 9.—Some radiolarian tests highly magnified. 1. Ceratospyris. 2. Hexalonche. 3. Theocapsa. 4. Ceratospyris. 5. Artopilium. 6. Cromyodrymus. 7. Podocyrtis.

3. **Class Tripylaria** (Phaeodaria) so named because the double-capsule membrane has a large (astropyle) and two small (parapyles) openings. In this class, the skeleton is often flask shaped and consists of hollow siliceous spicules which are not fused to form a rigid framework, and consequently it falls to pieces when the animal dies and so has furnished no fossils.

4. **Class Monopylaria** (Nassellaria) named from the Greek words meaning "single opening." The capsule is single and has but one opening; hence, the skeleton is arranged around a single axis and tends to be conical. This class has furnished numerous fossils, and examples are shown in Figs. 9^1, 9^3, 9^4, 9^5, and 9^7.

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CHAPTER III

THE PORIFERA OR SPONGES

We have seen that the distinctive character of the Protozoa was that the individual was a single cell and that all of the Protozoa which occur as fossils have skeletons of lime or silica, so there is slight likelihood of confusing them with any other kinds of organisms. In the balance of the animal kingdom the individual is made up of a large number of constituent cells, and these cells are differentiated in two or more groups, which, in the higher animals, become very complex both in the structures to which they give rise and in the functions which they perform.

Although several kinds of Porifera or sponges are mentioned by Aristotle, they have been understood only in recent years. Their fixed character, irregular growth, and almost total lack of perceptible movement prevented definite proof that they were not plants until the advent of microscopical investigation, which, so far as the sponges are concerned, dates from about 1850.

They are all aquatic and mostly marine and range in size from tiny forms just visible to several feet in diameter. They are, for the most part, indefinite in size and shape and take the form of platters, domes, fans, cups, goblets, trees, toadstools, trumpets, the same species differing in shape according as it grows in quiet deep or rougher shallow water. Their external form is largely conditioned by their environment and rarely indicates their relationship. The entire body of the sponge is penetrated by a more or less complicated canal system beginning at the outer surface of the body as numerous inhalant pores and, after traversing the body, emptying into one or more larger canals opening in the upper part of the body as one or more exhalant pores or oscula. This water circulation is maintained by the activity of certain cells, each of which has an outer rim or collar and from the center of which a long flagellum or whiplike process projects. It is the beating of these innumerable flagella that keeps the water in motion, and these cells perform the additional function of acting as food catchers and stomachs. These collared

cells with their flagella are known as "choanocytes," and they are very similar to the soft-bodied Protozoa known as the "Choanoflagellata"—so similar, in fact, that many naturalists believe that the sponges were originally derived from some form of Protozoa similar to the existing choanoflagellates.

The outer surface of the sponge body, and all inner surfaces where the choanocytes are absent, is covered with a single layer of epithelial pavement cells. The space between the canals is occupied by a slimy ground mass known as the "mesoglœa." In this are embedded various tissue cells and amœboid cells (leucocytes) as well as the cells (scleroblasts) which secrete the skeleton. The accompanying enlarged diagram through the body wall of a sponge will make clear these tissues (Fig. 10). On the inside are the choanocytes with their collars and flagella; on the outside is the layer of pavement cells; and between the two is the watery mesoglæa. The skeleton is made up of units known as "spicules," which may be calcareous, siliceous, fibrous (of spongin), or a combination of silica and silky spongin. The spicules may lie loosely scattered between the canals, or they may be more or less articulated together—the degree to which they are compacted into a rigid whole determining the durability of the skeleton and the probability of its fossilization.

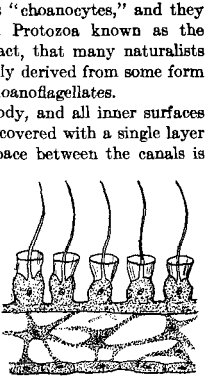
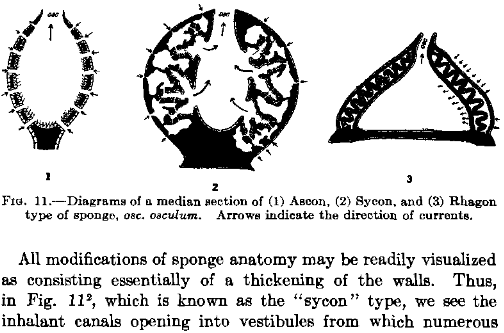


FIG. 10.—Greatly enlarged section through the body wall of a simple sponge, showing the collared cells, choanocytes, on the inside and the pavement cells on the outside, with the mesoglæa in between.

Although budding is common, probably all sponges also reproduce sexually. The fertilized egg cell by segmentation gives rise to a free-swimming larva, which soon attaches itself and becomes modified to the adult condition. Since paleontologists can study only the skeletons, the details of sponge anatomy may be left to biologists, but a few additional explanations are necessary in order to grasp the ground plan of the sponge as a whole and the manner in which it maintains life.

All sponges may be considered as variations or modifications of a simple saclike or urn-shaped body, such as is shown in Fig. 11[1]. The walls are regularly perforated with inhalant canals; the water is drawn in through these by the action of

the choanocytes which line the sac and which by beating the water cause a slow current upward and out through the osculum. The pavement cells constitute the outer covering of the sac, and the mesoglæa is shown in solid black. We might consider the cavity of the sac as a sort of stomach in such a type, since its lining of choanocytes catches and digests the food material suspended in the water currents, but in the more complex types derived from this simple, or "ascon" type, as it is called, the choanocytes no longer occupy the interior cavity, which then becomes lined with pavement cells and cannot be termed a stomach. We may call this cavity by the non-descriptive name of "atrium."



1 2 3

FIG. 11.—Diagrams of a median section of (1) Ascon, (2) Sycon, and (3) Rhagon type of sponge, *osc. osculum*. Arrows indicate the direction of currents.

All modifications of sponge anatomy may be readily visualized as consisting essentially of a thickening of the walls. Thus, in Fig. 11², which is known as the "sycon" type, we see the inhalant canals opening into vestibules from which numerous canals lead to special chambers lined with choanocytes, and the water, after running the gauntlet of the choanocytes, flows into the central cavity and out through the osculum. Figure 11³ illustrates an arrangement known as the "rhagon" type, which is characteristic of the siliceous sponges. Here the water current enters vestibules through numerous inhalant canals in the outer walls, passing by numerous tiny canals into small spherical chambers lined with minute choanocytes, then onward through tiny canals to inner vestibules, from these into the central cavity, and out through the osculum.

We may now turn our attention to the skeleton, which is the only part of the animal that is found fossil except in the rare

instances in which the whole body is preserved as a flattened and crushed impression. The skeletal units, or "spicules," as they are called, may be simply scattered about in the flesh, in which case they will be simple in form and, when the animal dies and rots, will fall to the bottom and be preserved as a matted mass without any definite arrangement. In the more complicated types of sponges, the spicules may be quite regularly arranged, chiefly with relation to the canals of the sponge body, and these spicules may be variously interwoven or consolidated to form a more durable skeleton more readily preserved as a fossil.

The spicules, which are often beautiful in form and show an almost infinite variety of detail, are of four general sorts. The first and simplest of these are those spicules which have but a single axis. They are, therefore, called "uniaxial," or "monaxons,"* and they may be straight, like needles or rods, or bent, like a hook, and they may be smooth or prickly or knotty. When calcareous they will be solid; when siliceous, they will have a tiny canal in their interior.

The second type comprise those spicules with four axes, in consequence of which they are known as "tetraxial," or "tetraxons." These are normally of four equal axes, three of which are in one plane 120 degrees apart, and the fourth is at right angles to these three (Fig. 12^1). This type is frequently modified by lengthening the fourth axis (Fig. 12^7) or by expanding the three axes in the one plane until the whole looks like a thumb tack (Fig. 12^3) or by curving and forking of the three axes until the whole looks like a chandelier or candelabra (Fig. 12^2) or by the elimination of the fourth axis resulting in three-rayed spicules (Fig. 12^8) or by leaving just the disk of the thumb tack (Fig. 12^{10}).

A third type known as "hexactinellid" consists of six axes or rays at right angles to each other (Fig. 12^9) and is exactly like the iron jacks with which children play their game of jacks. This type affords a most efficient unit for building a durable skeleton, as may easily be seen, since, if the ends of the axes are fused to the ends of the axes of the adjacent spicules, there results a solid latticework with cubical meshes. It is of these hexactinellid spicules that the beautiful siliceous skeletons of the so-called "glass sponges" are built, as, for example, the so-called "Venus' flower basket" and "Neptune's goblets."

* Single axis (English) = uniaxial (Latin) = monaxon (Greek).

A fourth type of spicule, which is often regarded as a modified tetraxon, characterizes an order known as the Lithistid sponges, which are among the most abundant fossil sponges. These spicules are known as "desmons" and are characterized by their rootlike processes by means of which they become interlocked and fused to form massive stony skeletons whose durability doubtless accounts for their abundance in the rocks. Three of these are shown in Figs. 12[11–13], and Fig. 12[13] shows how they are soldered together to form almost solid walls around the canals.

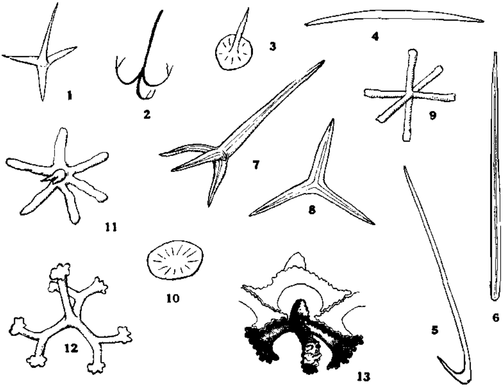


FIG. 12.—Different forms of sponge spicules, highly magnified.

THE CLASSIFICATION OF SPONGES

Class I. Myxospongia.—Soft bodied with only scattered flesh spicules—no fossils.

Class II. Ceratospongia.—*In which the skeleton consists of silky* or horny fibers which are crushed when buried by sediment and, hence, do not furnish any surely recognizable fossil forms.

Class III. Calcispongia.—With one-, three-, or four-rayed solid calcareous spicules—three-rayed commonest, four-rayed rarest. Rarely forked or modified. Orders Ascones, Sycones, Leucones, and Pharetrones.

Only the second and fourth orders furnish recognizable fossils. The Sycones are mostly small, delicate, shallow-water forms with regularly

arranged spicules and walls with simple radial canals. They are relatively rare as fossils but occur sparingly from the marine Carboniferous down to the present.

The Pharetrones have thick walls and a complicated canal system, and their spicules are united to form a rigid framework. They are found, usually in limestone deposits, from the Devonian to the present.

Class IV. Silicispongia.—Spicules siliceous with axial canals or of silica enclosed in spongin. Here belong the majority of fossil species.

Subclass Triaxonia or Hexactinellida.—Cambrian to Recent. Spicules six rayed normally intersecting at right angles, detached or fused.

Order Lyssacina.—Spicules detached or but partially fused.

Order Dictyonina.—Spicules fused, but their axial canals interrupted between spicules.

Subclass Demospongia.—Spicules of one or four rays.

Order 1. Monaxonia.—Spicules uniaxial often enclosed in spongin, never fused; hence, only recognized as fossils by their detached spicules which are needles, pins, hooks, or cylinders.

Here belong the majority of existing marine sponges and the few fresh-water forms (Spongilla). Detached spicules of these types have been recognized from the Silurian to the Recent.

Order 2. Tetraxonia.—Spicules four rayed or its modifications, not fused. Represented by detached spicules from the Jurassic to the Recent.

Order 3. Lithistida.—Spicules modifications of the four-rayed spicules of the Tetraxonia but fusing to form massive skeletons, often found fossil. These are the most abundant fossil sponges and comprise numerous species and genera grouped in five suborders and occurring from the Cambrian to the Recent.

RELATIONSHIP OF THE SPONGES

Paleontologists have been prone to consider the sponges as a division of the phylum Cœlenterata, but this is not the case. They differ from all the Metazoa in lacking the exact homology of ectoderm, mesoderm, and endoderm. They differ from the Cœlenterata in their canal system, in their choanocytes, and in lacking the sense organs of the cœlenterates. Sponges have no muscular or nervous systems and only a vague general sensibility. They were undoubtedly derived from the Protozoa in pre-Cambrian time, and their ancestors must have been something like the existing Choanoflagellata. The sponges have come down through the ages with but relatively slight modifications and have never given rise to other or more advanced groups of organisms.

CHAPTER IV

CŒLENTERATA

The Cœlenterata are aquatic, and the majority are marine. They include such familiar living forms as hydras, jellyfishes, corals, and sea anemones and embrace a host of extinct forms, among which the extinct group of graptolites is very important in determining horizons in the older Paleozoic rocks.

The cœlenterate body is essentially a hollow sac with an opening commonly called the "mouth," although it is the only opening to the body and serves not only for the entrance of food and water but also for the exit of all waste and sexual products. This saclike body may be spherical, cylindrical, or disk shaped, and its opening is surrounded by tentacles, so that the whole has a superficial radial symmetry. The sac consists of an inside (endoderm) and an outside (ectoderm) layer, between which may be developed a middle layer, but this is frequently absent and usually feebly developed. The outer body layer and, less often, the inner body layer develop cells known as "cnidoblasts" filled with an irritating or poisonous fluid and containing a spirally coiled filament (the nematocyst). The whole has a sensory projection on the outside which when touched acts like a trigger in releasing the filament which shoots out like a released watch spring along with the poisonous fluid and doubtless paralyzes any small organisms with which it comes in contact, and these serve as food.

The Cœlenterata are a very old group and are considered to have originated from a protozoan somewhat like the existing Dinoflagellata. At first, they may have been something like their modern free-swimming larval stage, known as a "planula." Early in their history, they separated into two main evolutionary lines—one prevailingly sessile, and the other free swimming. The sessile line adopted that curious alternation of sexual free, and non-sexual sessile, generations, and the latter grow by various methods of budding into colonial or compound organisms and constitute the generation which contributes to the paleontologic record by becoming fossilized.

They may not secrete any hard parts, in which case they are usually not preserved in the rocks, but a large number, including the common fossil forms, secrete a horny or calcareous skeleton—the latter often very compact and stony.

The Cœlenterata differ from the Porifera in lacking pores, canals, and choanocytes and in having muscular and nervous systems, as well as sensory tentacles and cnidoblasts. They are distinctly more individualized than sponges and, in their movements, and reactions to external stimuli, show that they are on a considerably higher plane of organization.

Systematists are not entirely agreed as to how they should be classified or on the exact relationship between their various divisions. In this book, the following five classes are recognized: Anthozoa, Graptolitoidea, Hydrozoa, Discophora, and Ctenophora. The great bulk of the fossil forms belong to the first three of these five classes—the Discophora being rarely, and the Ctenophora never, found fossil.

CLASS ANTHOZOA

The Anthozoa include those forms, commonly called "corals," with horny, calcareous, or partly horny and partly calcareous, skeletons, as well as those entirely soft-bodied existing forms known as "sea anemones."

The name Anthozoa means "flower animals," and although the red coral of the Mediterranean has been an article of commerce since the earliest times, the animal nature of corals was not discovered until 1727.

The Anthozoa are exclusively marine and predominate in shallow water—the reef corals in depths up to 200 feet and in temperatures not below about 65° Fahrenheit. Only a few of the Anthozoa are entirely soft bodied, the majority secreting individual skeletons (coralla), and this is practically the only feature distinguishing them from sea anemones. The simplest form of corallum is made up of quantities of microscopic calcareous units, which may remain detached or may unite into tubular forms, or the secretion may be confined to the basal part of the animals, in which case a solid axis (sclerobase) is formed. This axis in life is covered with a soft, living substance (cœnosarc) in which the individuals are embedded.

In the stony corals and some others, a compact calcareous skeleton is secreted by the ectoderm. In a living coral, when

the polyps are extended, it looks as though the skeleton was internal, but it is really external.

The animal itself is columnar in form and bears a crown of few or many tentacles on the end opposite to that by which it is attached. Within this ring of tentacles is a muscular area known as the "peristome" in the middle of which is a slitlike opening usually called the "mouth." This does not open directly into the interior of the saclike body, as it does in the Hydrozoa, but hangs down as a short tube (the stomodæum), one or both ends being provided with cilia used to induce currents. The cavity of the sac, or cœlenteron, is the place where the functions of digestion, circulation, excretion, and reproduction are performed.

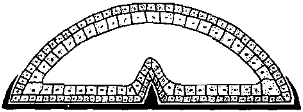


FIG. 13.—Greatly enlarged section of the first stage of attachment of a hexacoral, showing the double-walled body. The basal plate, columella, and *beginning of the walls in solid black.*

The saclike body is not simple, as it is in the Hydrozoa, but is folded radially to form what are called "mesentaries," much as a thin cloth sack would fold if the mouth were shirred and the bottom pulled. Reproduction is both sexual and asexual. In the first method, a free-swimming larva known as a "planula" is formed, which subsequently attaches itself to some foreign object. In the second method, new individuals are formed by budding. A considerable number of kinds of budding are distinguished according to the part of the parent from which the bud develops.

The skeleton, which is the only part fossilized, is naturally the part that is of most interest to the paleontologist. This skeletion may be most easily understood by following its formation in the existing Hexacoralla. When the free-swimming larva attaches itself, it flattens out like a tiny thin biscuit and secretes a calcareous disk—the basal plate. Sometimes, the central part of the soft base pulls away from the calcareous basal plate, secreting a peglike central calcareous column known as the "columella" (Fig. 13). When still very young, the basal part develops 12 radial folds between which bladelike radial upgrowths from the

basal plate are secreted. These are the primary septa and serve as partitions between the 12 primary mesentaries of the soft body sac. The outer edges of the septa are united by a wall or theca. With the growth of the animal the body folds midway between the septa forming secondary mesentaries and secreting secondary septa in each fold. There may be several cycles of foldings with the resulting mesentaries and septa, the number being a multiple of the number of primary mesentaries and septa. The resulting skeleton is known as a "corallum." In simple forms, the foregoing will be all the hard parts developed, but most corals are not so simple and show other calcareous structures. These are either strengthening structures, such as the tiny calcareous cross-bars which run tangentially from one septum to its neighbor and which are known as synapticulæ; or they may be somewhat dissimilar calcareous fillings of the earlier and older part of the corallum as the animal grows upward, as if the animal each season added a story to its house and filled in the lower stories with calcareous dèbris, always living in the top story. When this filling is in the form of tiny calcareous plates without arrangement, they are known as "dissepiments," and in an old corallum where dissepiments are numerous, the basal part for an inch or two will be filled with a vesicular mass known as "endotheca." Sometimes, instead of being without arrangement, the dissepiments will be more or less in transverse layers, and when this arrangement is perfect, they will form transverse partitions or floors which are then known as "tabulæ." Tabulæ are especially developed and characteristic in those corals like the Tabulata or some of the Octocoralla, like the existing organ coral in which the corallum is narrow and very long and in which septa are vestigial or absent.

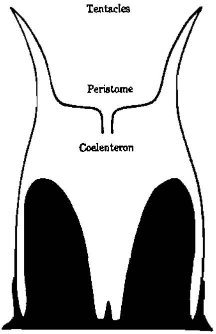


FIG. 14.—Median longitudinal section of a coral showing soft parts in outline. Calcareous walls, septa, and columella in solid black.

Difficulties in understanding the hard parts arise chiefly because these various hard parts show intermediate forms, or

some of the calcareous parts may be resorbed, or the individuals of a colony may not secrete calcareous walls between many of the individual polyps.

Four subclasses of Anthozoa may be recognized. These are the Tetracoralla, Hexacoralla, Octocoralla and Tabulata.

Tetracoralla

The Tetracoralla are all extinct and are not known in rocks younger than the Paleozoic. They include both solitary and colonial forms and have their septa arranged in fours or multiples of four (hence, the name Tetracoralla). Dissepiments are usually formed; the walls are well developed, usually wrinkled, and are thought to have been formed by the thickened and fused outer edges of the compact septa. Their coralla may be radially symmetrical, but in many of the solitary cornucopia-shaped forms, some of the septa are more developed than others, and there are a variety of changes in septal arrangement during life brought about by the resorbtion of old and the secretion of new septa. The tetracorals appear in the geological record in Ordovician times, reach a maximum in the Silurian and Devonian, and disappear in the Permian.

The solitary tetracorals, which reproduce only sexually, are often called "cup corals" and are about the shape and size of a short-horned cow's horn. They were attached by their small end. By grinding cross-sections, the various stages in their life history can frequently be made out. In the adults, the septa may be radially arranged and all alike, or certain of them may be thicker and otherwise differentiated. A common arrangement is one in which two opposite pairs of septa are thickened. One long, straight septum on the convex side of the corallum is called the "cardinal septum." Opposite the cardinal and, consequently, on the concave side of the corallum is a narrow thick septum called the "counter." On each side, about midway between the cardinal and counter, is a thick, curved septum called the "alar." There may be thin septa between the alar and counter and between the alar and cardinal, the latter running from the outer wall to the cardinal septum. Sometimes the counter septum is in a depression known as a "fossula." In the colonial tetracorals the form of the colony is largely dependent on the method of budding. If a bud forms within the corallum

and quickly expands to the diameter of the parent, the latter is smothered, and a long cylindrical column is formed of a succession of individuals one above the other. If several buds start in an older corallum, the whole colony will become a much-branched affair with live animals in only the end coralla of the branches.

The reason for the total extinction of the tetracorals or their relationship to the contemporary or later corals is entirely uncertain.

Hexacoralla

The hexacorals are solitary or colonial forms with their septa in sixes, twelves, or multiples of six (hence, their name). They include the reef-building and solitary deep-water corals of the present seas, the entirely fleshy sea anemones, and the corals

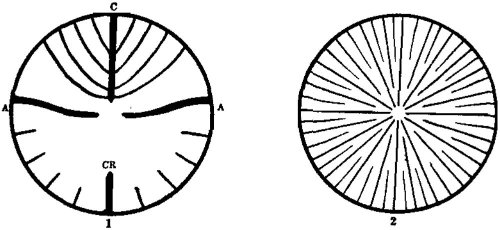


Fig. 15.—1. Cross-section of a tetracoral. *c*, cardinal septum; *cr*, counter-septum; *a*, alar septa. 2. Cross-section of a corallum of a hexacoral, showing cycles of septa.

with a horny (non-calcareous) axis. Only the first of these, known as the Madreporaria or "stony corals" are sufficiently permanent to furnish fossils. They appear in the Triassic and are the typical corals of present-day seas. They are readily distinguishable from the tetracorals and octocorals by the strictly radial arrangement of their septa in sixes (Fig. 15[2]), and the living animals are distinguishable from the living octocorals by having as many cycles of tentacles as there are cycles of septa and by these tentacles' being simple and not plumose. They vary greatly in size and form, the character of the colony depending on the close packing of the coralla or the formation of a calcareous ground mass between the individual coralla.

The method of budding largely determines the resulting form. Thus, in some of the genera of the family Fungidæ the new buds form on the outer walls of the parent and the whole colony looks something like a bracket fungus. Another manner of colony formation by non-sexual methods is known as "fission" and is not uncommon in this subclass. In this, the animal gradually divides by widening in one dimension and becoming constricted at right angles to it. This process is reflected in the hard corallum by its assumption of an elliptical cross-section and final division to form two coralla (Fig. 16). Among certain Mesozoic and later forms, fission may not result in the complete separation of the individuals which remain united basally and consequently do not secrete partition walls. This results in an arrangement of the hard parts in meandering furrows, and their superficial appearance has suggested the name "brain corals" that is frequently applied to them. It is made clear in Fig. 17.

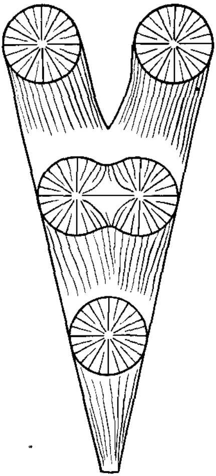


FIG. 16.—Diagram showing the formation of two individuals from one by fission in a Mesozoic hexacoral.

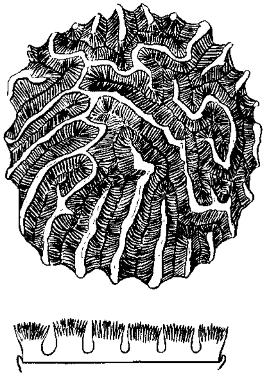


FIG. 17.—A brain coral. Skeleton of a colony above and a row of only partially separated polyps below.

Octocoralla or Alcyonaria

The octocorals are almost exclusively colonial forms. They make their appearance in the Ordovician and continue in existing seas. They are never abundant fossils, largely because the hard parts are not integrated to form as compact skeletons as in the other groups. The calcareous units of which the skeleton is composed (sclerodermites) may remain detached from one another or may be closely packed to form an axis (sclerobase) about which the polyps were distributed, or sometimes they become united to form regularly partitioned tubes. The octocorals include the sea pens, dead-men's-fingers, organ coral, and sea fans of existing seas, none of which is certainly known in the fossil state. The living animal has hollow, plumose tentacles, never more than eight in number. The only families furnishing any considerable number of fossils are the Helioporidæ and Heliolitidæ. These both form massive colonies characterized by small tubular cavities with tabulæ and faintly developed septa and by tubes of two sizes the inhabitants of which show division of labor among the polyps of the colony. The larger holes, called "autopores," are inhabited by functional individuals with tentacles. The small holes, called "siphonopores," are occupied by small, incomplete individuals without tentacles and connected by a surface living layer with the larger complete individuals (Fig. 18).

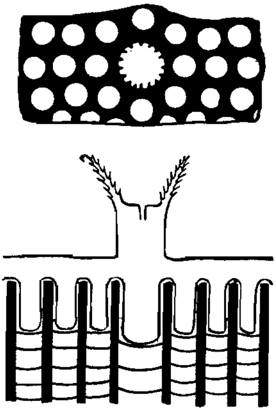


Fig. 18.—An octocoral, Heliopora. Surface view of skeleton above showing an autopore and several siphonopores. Section below showing an autopore and several siphonopores with their tabulæ, and outlines of a complete tentacled polyp and several siphonopolyps connected with it by a living layer of soft tissue.

Tabulata

The tabulate corals constitute a large and important group, considerable rock formers during the middle Paleozoic, a few lingering on in the Mesozoic. They are invariably colonial and are characterized by long, slender coralla, tubular in cross-section or prismatic when closely packed; the latter (Favosites and its

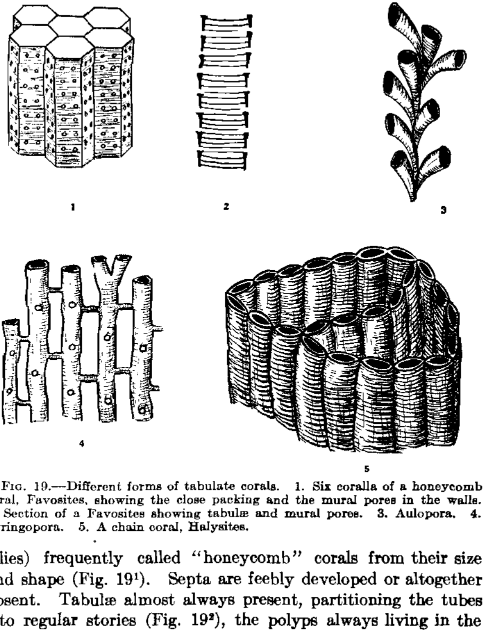


FIG. 19.—Different forms of tabulate corals. 1. Six coralla of a honeycomb coral, Favosites, showing the close packing and the mural pores in the walls. 2. Section of a Favosites showing tabulæ and mural pores. 3. Aulopora. 4. Syringopora. 5. A chain coral, Halysites.

allies) frequently called "honeycomb" corals from their size and shape (Fig. 19^{1}). Septa are feebly developed or altogether absent. Tabulæ almost always present, partitioning the tubes into regular stories (Fig. 19^{2}), the polyps always living in the uppermost story. The walls are thick and are frequently perforated by large pores known as "mural" pores. The tabulate corals get their name from the tabulæ which are such a prominent feature of their skeletons. They appear in the Ordovician, and

all of the families have a long range except the Halysitidæ (Fig. 19[5]) or chain corals, which are confined to the Ordovician and Silurian and in which the coralla are united in rows and somewhat resemble the links of a chain as their ends are seen on weathered rock surfaces.

In the genus Aulopora (Fig. 19[3]), each corallum is small and trumpet shaped, with thick, imperforate, wrinkled walls. New coralla are formed by basal budding, and the whole colony is prostrate and attached to some foreign object. In more advanced genera—Romingeria, for example—only the early stage is prostrate, the mature colony becoming more or less erect and bushy.

In Syringopora and its immediate allies, the coralla are somewhat flexuous and thin-walled tubes, with an early, prostrate, Aulopora-like stage but soon becoming erect and with cross-connections, as shown in Fig. 19.[4]

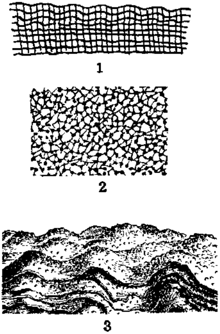


FIG. 20.—1. Magnified vertical section of a stromatoporoid showing radial pillars and laminæ. 2. Horizontal section. 3. Surface view.

CLASS HYDROZOA

Attached polyps or polyp stocks in which the body sac is simple and not radially folded, as in the Anthozoa; the opening into the sac a simple hole and not tubular, as in the Anthozoa. Marine or more rarely fresh-water animals, which rarely secrete hard parts. Averaging smaller in size and simpler in organization than the Anthozoa and usually rare as fossils. The existing forms are characterized by a dimorphism or polymorphism of the individuals of the colony, some being adapted for feeding, some for protective, and some for reproductive functions. They also show an alternation of generations—the colony formed by non-sexual budding giving rise to free-swimming medusæ (sexual individuals) whose progeny start new colonies.

Several existing orders are recognized, but the only orders that have furnished recognizable fossils are the Hydrocorallinoidea, Tubularoidea, and Stromatoporidea.

The Hydrocorallinoidea have naked polyps which secrete a vesicular base into which they can retract. This base somewhat resembles the skeleton of such an octocoral as Heliopora but is less compact and is unknown in rocks earlier than the Tertiary.

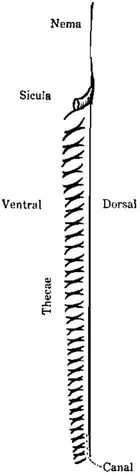


FIG. 21.—Diagram showing the parts of a Graptolite stock or rhabdosome.

The Tubularioidea polyp is also naked or covered with a horny covering. It secretes a horny or calcareous base found encrusting a dead shell or other foreign object. These layered encrusting sheets have been found fossil occasionally from the Triassic to the present but are of slight interest or importance.

THE STROMATOPOROIDS

The Stromatoporoidea, which are allied to the preceding, are of greater interest since they are abundant enough to form large nodular or reeflike masses during the Paleozoic, especially during Silurian and Devonian, times.

They formed many concentric wavy layers of calcite connected by tiny rods (radial pillars), the units of both rods and layers (laminæ) being fibrous, either hollow or solid, and forming a felted mass (Fig. 20). They offer great difficulties to the student and are usually differentiated into two groups, one in which the fibers are solid (Actinostromidæ) and the other in which the fibers are hollow (Stromatoporidæ). The genera in each are based on such features as the surface ornamentation of the layers, on whether the laminæ are flat or undulate, and on whether the pillars extend between but two or through several layers. Sections have to be ground and studied microscopically in order to identify them properly, and they have never been popular objects of study among paleontologists.

CLASS GRAPTOLITOIDEA

The graptolites, which are especially characteristic of the later Cambrian and early Ordivician, reached an early maximum and, except for a few stragglers in the Devonian and earlier Carboni-

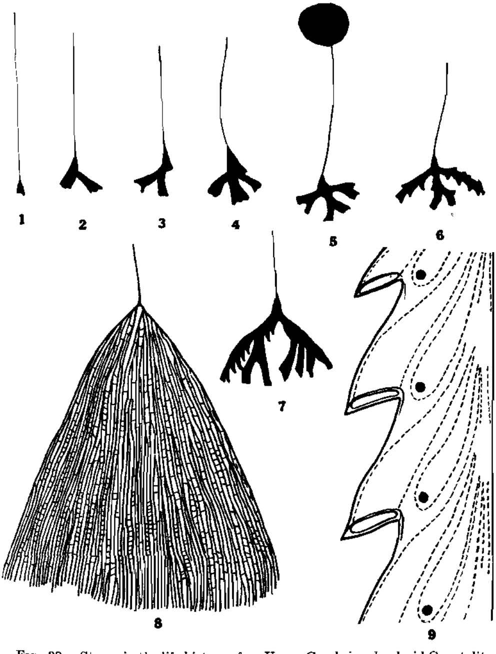


FIG. 22.—Stages in the life history of an Upper Cambrian dendroid Graptolite, *Dictyonema flabelliforme*. 1. Sicula with its extraordinarily long nema. It probably had a primary disk in this and all subsequent stages, but the disk is frequently not preserved. 2. Similar sicula, fully grown and giving off a lateral theca. 3. Sicula with two thecæ. 4. Sicula with three thecæ. 5. Sicula with its primary disk and with six thecæ. 6. More advanced stage in which the lower branch has forked. 7. A still more advanced stage showing the first formed dissepiment between the two left branches. (Figures 1 to 7 are five times life size.) 8. A normal mature colony, life size. This is funnel shaped or conical, the branches irregularly united by dissepiments, and the apertures of the normal polyps (thecæ) opening on the inside of the branches. 9. Much enlarged view of a single branch from the side, showing outline of the axis and thecæ and of the internal cavities and gonothecæ. Gonothecal apertures on the lateral surface. (Figures 1 to 8 *after Ruedemann*, Fig. 9 *after Swinnerton*.)

iferous, became extinct during Silurian time. At the time of their greatest abundance they varied rapidly and many became world wide in their distribution, so that they are important index fossils.

They sometimes occur in vast numbers in the early Paleozoic rocks but are usually preserved in a very imperfect state, being found lying flattened along the bedding planes of the dark, shaly rocks, looking like coaly scroll-saw blades. More rarely, they are found in limestones, and they may then have the internal cavities filled with calcareous or other mineral matter and preserve more or less their living form.

Since they have been so long extinct and are not represented by any very closely allied existing animals, they long defied naturalists' attempts to understand their structures and habits, and they have frequently been confused with algæ, bryozoans, sertularians, plumularians, and sponges. None secretes calcareous or siliceous parts, and their skeletal tissue (generally termed periderm) is a somewhat flexible, horny material (chitin) generally dense but sometimes in the form of a network (Retiolites). They were strictly marine and colonial, and a colony originating by budding from a single initial polyp has been variously termed a "polypary," "rhabdosome," or "stock." Such a colony (rhabdosome) originates from a single polyp whose tiny conical or dagger-shaped skeleton is called a "sicula" and is attached by its hollow, threadlike, more or less extending tip (nema). By the formation of a succession of buds which develop into polyps, a colony grows in a linear, biserial, or tetraserial arrangement, branching in various ways. The skeletons of the members of the colony are called "thecæ" (they have at various times been termed cells, cellules, calycles, denticles, cups, hydrothecæ). They are always small and usually conical or cylindrical in form and usually are arranged with their walls in contact, opening at their bases into a common canal. Their apertures may be simple or contracted, and in some of the more specialized forms they may be furnished with tiny spines.

The simpler, earlier forms were sometimes attached to the sea bottom but more often to floating objects, especially seaweeds. The later more specialized forms developed a float of their own and were distributed by ocean currents.

This class may be divided into two subclasses—the Dendroidea and the Graptoloidea.

The first and less progressive group (Dendroidea) consists of frondlike colonies, fan or funnel shaped, consisting of many branches often connected with one another in a network by delicate, horny outgrowths (dissepiments). They range from the later Cambrian to the early Carboniferous but were never so abundant as the Graptoloidea, nor are they so important as indicators of horizons. The long-ranging genus Dictyonema is the best known and may be considered as typical for the whole subclass. The sicula has a long nema and a primary disk by which it was attached. Several early stages of growth by the formation of successive buds are shown (Figs. 22^{1-7}). At maturity, the colony is funnel shaped and 2 or 3 inches long, hanging down in the water (Fig. 22^{8}). The apertures of the normal polyps are on the inside surface of the funnel. It has been shown that each generation of buds produced a normal polyp, a sexual individual (gonangium) which remained internal and communicated with the exterior through pores on the sides of the branches, and an internal budding individual which repeated the whole process in the next generation. A view of a much enlarged branch from the side (Fig. 22^{9}) will make this clear.

The second subclass (the Graptoloidea) comprises the more progressive graptolites. Only one kind of buds has been observed. The Graptoloidea is divided into two orders—the Axonolipa and the Axonophora.

The Axonolipa comprise those forms in which the whole colony is derived by budding from a single sicula and in which the thecæ are arranged in a uniserial or biserial row with their apertures directed away from the sicula. Their general organization may be understood from the accompanying figures of some of the stages in the life history of the genus Goniograptus (Fig. 23). The Axonolipa are usually divided into the three families Dichograptidæ, Leptograptidæ, and Dicellograptidæ, and a great many genera and species have been described. They appear to show three series of evolutionary changes: (1) a change in the attitude of the branches from pendant to erect; (2) a modification of the thecæ, especially around the apertures; and (3) a simplification of the branching: thus, the genus Loganograptus has 16 branches, Dichograptus 8, Tetragraphus 4, and Didymograptus 2.

The order Axonophora is characterized by a general lightening of the colony and by the frequent formation of a float from which

the colony was suspended in the water. The budding polyps grow backward along the lengthening nema away from the sicula and their apertures point toward the attached end—oppositely from what they do in the Axonolipa. The colony develops a single or double strengthening axis or rod known as a

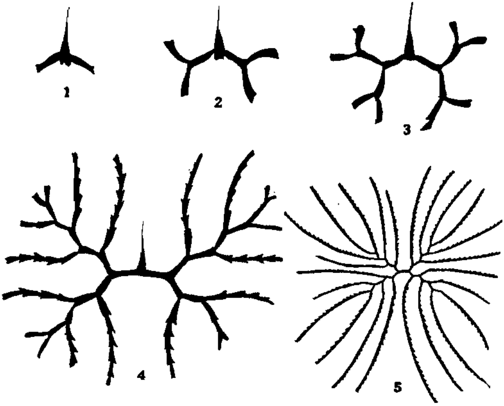


FIG. 23.—Stages in the life history of an Axonolipous graptolite, Goniograptus. (*After Ruedemann.*) 1. Young rhabdosome showing the sicula and its nema and the first two thecæ. 2. Each of the first thecal buds have given off a lateral bud. 3. The buds of the second order have originated those of the third order, thus outlining the central forked stalks of the mature colony. The lower right-hand bud of the third order has budded a denticulate theca like all of those that subsequently develop. 4. An adolescent colony, fully branched, showing the normal denticulate thecæ. Subsequent growth merely lengthens the branches. (Figures 1 to 4 are five times life size.) 5. Mature colony, life size. The early stages of all of the multiramous Dichograptidæ are probably like those of Goniograptus.

"virgula," which runs along the back of the common canal. The thecæ are arranged uniserially or biserially, and the colony is not a rhabdosome developed from a single primary sicula, but, in addition to the primary rhabdosome, additional rhabdosomes develop from sexually developed siculæ which retain their connection with the parent colony—the whole frequently being called a "synrhabdosome." The structure and relationship of an

axonophorous graptolite may be understood from the following life history of the genus Diplograptus:

Life History of Diplograptus.—The young sicula when it is liberated from the gonangium of the parent is attached by its apex to a little square (node) in the center of a double plate. During subsequent growth this plate becomes inflated to form the horny float (basal cyst). Meanwhile, the sicula gives off a lateral bud which commences to grow downward and then turns outward at a right angle to the sicula; this, in turn, gives rise to a second bud, the third polyp, which grows alongside and in the opposite direction from that of the sicula. Then a lateral bud is given off from the sicula opposite the first, and two rows of polyps are gradually budded in two rows on opposite sides of the axis, and as these two rows grow up along the sicula the latter *gets farther and farther from the node* by the *lengthening of the* stipe or nemacaulis (corresponding to the hydrocaulis of modern Obelia), and this is strengthened by the secretion of a stiff rod in its wall (the virgula).

As the primary rhabdosome lengthens it resembles a two-edged band saw—this biserial arrangement of the polyps being known as "diprionodont" (doubly saw-toothed). The individual polyps are oriented back to back and in life were connected by an axial canal in whose wall the virgula gave a certain degree of rigidity to the whole.

Below the float there developed around the node oval enlargements corresponding to the blastostyle or gonotheca of a living hydroid. Within these gonangia there were developed siculæ (instead of medusæ, as in modern hydroids). Most of these remained attached, lengthening their stipes (nemacaulis), and, by budding, exactly as in the primary rhabdosome, gave rise to secondary rhabdosomes, which hung down from the float in clusters. Sometimes the siculæ in a gonangium developed tiny plates at their points of attachment and were then discharged into the water, floating away to start new colonies. Successive generations of gonangia around the node produced successive whorls of secondary rhabdosomes, which as they subsequently developed were of different lengths.

This life history, which is probably typical for all of the Axonophora, is best known in Diplograptus. It shows the following contrasts with the groups Dendroidea and Axonolipa: The nemacaulis, by the reversed direction of the budding polyps,

becomes incorporated in the axis of the rhabdosome; the primary rhabdosome thus formed is homologous with the entire colony of the Dendroidea or Axonolipa, as are also the later-formed secondary rhabdosomes, each of which originates from a single sicula (Fig. 24).

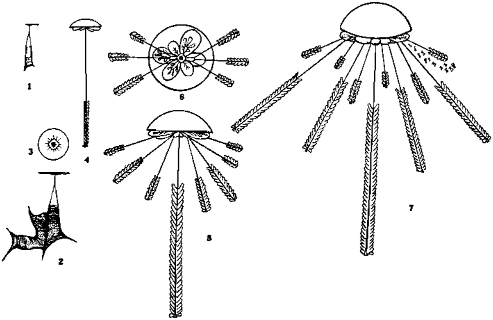


FIG. 24.—Stages in the life history of Diplograptus. (*After Ruedemann.*) 1. Sicula suspended by its node, showing growth lines. 2. Sicula with one lateral and an ascending theca with the disk beginning to inflate. 3. View of the disk of Fig. 2 from below, showing its node. 4. Somewhat older form, showing the float, gonangia budding around the node, and the double row of thecæ of primary rhabdosome suspended by the lengthening nemacaulis. 5. A more advanced colony, showing the primary rhabdosome, secondary rhabdosomes, and gonangia. 6. Same from below, showing the undersurface of the float, the gonangia surrounding the node, and several secondary rhabdosomes. 7. A mature colony, showing the same features, and also the liberation of a generation of free-floating siculæ. (All the figures enlarged.)

DISCOPHORA AND CTENOPHORA

Two classes of Cœlenterata remain to be mentioned—the Discophora and the Ctenophora. Both of these are entirely soft bodied and are popularly known as "jellyfishes." The Ctenophora are much modified oceanic forms, not known as fossils; and the Discophora, although their watery, jelly-like bodies are entirely unfitted for preservation, are occasionally preserved under exceptional conditions in fine-grained muds of various geological ages, such as in the Cambrian of Sweden and British Columbia and the Jurassic lithographic limestone of Bavaria. These occur as molds of the upper or lower surface or as mud casts of the gastric pouches, as in the Cambrian of the southern Appalachian region.

CHAPTER V

WORMS

Of all the larger divisions of the animal kingdom none is so poorly adapted for preservation as fossils as the worms, consequently no group has a more incompletely known geological record. In consequence, paleontologists are prone to use the old Latin term of *vermes* to include all wormlike animals, although it should be remembered that the worms exhibit a wide diversity of appearance, structure, habit, and relationships and comprise at least four great groups of the rank of independent phyla.

They are mostly soft bodied, bilaterally symmetrical animals in which the body may be unsegmented or segmented. The unsegmented worms have a dorsal and ventral body surface differentiated and may be flat or round in form. The flatworms, phylum Platyhelminthes (Greek for "flatworms"), is a very large group including the fresh-water planarians and such parasitic forms as liver flukes and tapeworms. The roundworms, phylum Nemathelminthes (Greek, meaning "threadworms"), is also a large group with many parasitic forms such as Ascaris, pinworms, trichina etc. Here belong the slender fresh-water worms responsible for the erroneous belief that horsehair put in water becomes alive.

In the third phylum Trochelminthes (Greek, meaning "wheel worms") are very tiny aquatic worms in which the cilia are arranged in circles, and their vibration gives the appearance of a rotating wheel.

With the rarest exceptions none of these three phyla of unsegmented worms is found fossil. Occasionally, an obscure impression will have been preserved in some fine-grained sediment, or their trails and tracks over an old sea bottom, or the casts of their burrows, may be fossilized. Sometimes, traces of parasitic forms will be recognized in fossil insects of the Carboniferous or in insects preserved in Tertiary amber.

The so-called "higher" or "segmented" worms, phylum Annelida, are characterized by having an elongated segmented

body with the mouth at one end and the anus at the other. Their only fossil representatives belong to the class Chætopoda so named because the body has bristle-like locomotor appendages on the body segments. (The name comes from the Greek words meaning "bristle" and "foot.") This class includes earthworms which are unknown as fossils, the free-swimming marine worms, and the tube-forming marine worms. Under exceptional conditions of preservation, as in the middle Cambrian Burgess shales of British Columbia, fairly complete impressions of these soft-bodied organisms can be recognized. More often, their trails or their tiny, horny jaws are preserved. They are obviously very ancient and are of great theoretical interest as the probable ancestors of the Arthropoda phylum.

The group known as Tubicola or Sedentaria embraces more common fossils because of their habit of secreting a calcareous protective tube; this may be irregular or coiled, attached or free. These fossils are sometimes abundant enough to give their name to the enclosing rock, as in the case of the Lower Cretaceous Serpula limestone of Germany. Fossil worm tubes are known from the Ordovician to the Present, the commonest genera being Serpula and Spirorbis. Little can be determined about the inhabitants of these fossil worm tubes and they are, therefore, more interesting than they are instructive.

CHAPTER VI

ECHINODERMA

The great phylum of Echinoderma (often improperly called the Echinodermata) comprises not only such familiar existing animals as the sea urchins, sea stars, sea cucumbers, and serpent stars but also the less familiar sea lilies and a host of extinct forms going back to the oldest fossiliferous rocks and including some of the most beautiful fossil forms.

It shows a great diversity of form and habits, but all except the wormlike sea cucumbers secrete a readily recognizable calcareous skeleton. Echinoderma share certain features in common, such as circulatory, water, and nervous systems; and differ from the Coelenterata in having a true alimentary canal; a body cavity; an external skeleton composed of plates (except in the sea cucumbers), which, in all except the most primitive forms, are definite in number and arrangement; an exclusively sexual mode of propagation; and in being exclusively marine. They all exhibit a more or less complete radial symmetry which is not confined to the skeleton but includes the various systems of soft organs within it—a conclusive proof that their ancestors were attached organisms, since all freely moving organisms tend to have a bilateral symmetry.

The organization of the echinoderm is essentially adapted to clear water, first as attached forms which would seek attachment on hard and not soft bottoms. The sea stars became adapted to softer bottoms by the development of papulæ on the upper surface for breathing. The only order of sea urchins which is essentially a soft-bottom specialization shows this adaptation in a variety of ways. Regular echinoids are hard-bottom forms moving with equal facility in any direction—hence, their radial symmetry. Many of them breathe by gills hanging down into the water around the margin of the peristome, which would function feebly or not at all on a soft bottom.

The irregular echinoids show the following soft-bottom adaptations: (1) elongation of body in many; (2) migration of

mouth forward in many (a much more advantageous position and due to their normal forward motion); (3) reduction and modification of the spines and development of spineless areas, thus reducing friction in an animal plowing over soft bottoms;

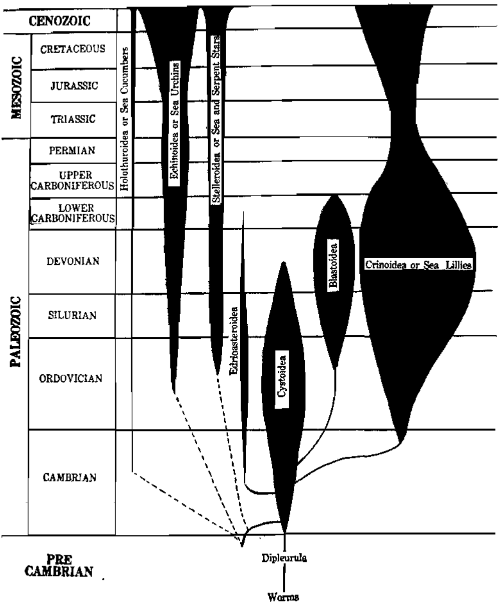


FIG. 25.—Diagram showing the geological history and the relationships of the different classes of echinoderms.

(4) modification of the podia of the petals for respiration on the highest and most advantageous part of the body and the loss of the peristomial gills on the underside of the body; (5) migration of the anus from the apical system toward the hind end of the body so that the waste products would not foul the

respiratory podia; (6) reduction in size of peristome and loss of jaws in one large group in which the lower (hinder margin) of the peristome acts like a scoop shovel taking in the organic mud as the animal moves forward, which serves as food.

Opinions differ as to how echinoderms should be classified. The accompanying diagram which summarizes their relationships and geological history shows the groups which are recognized in this book (Fig. 25).

The most ancient forms—the Cystoidea, Blastoidea, and Crinoidea—are commonly attached to some foreign object by a stem and are sometimes grouped together in one large group known as the Pelmatozoa, and it is this long-continued attached

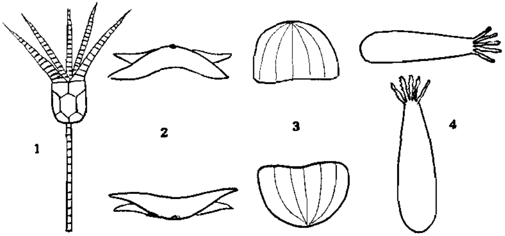


FIG. 26.—Physiological position (above) and morphological position (below) of 1. A crinoid. 2. A sea star. 3. A sea urchin. 4. A holothurian.

stage of racial history that gave rise to that radial symmetry which has persisted in the later free forms like the sea stars and sea urchins and the more abundant types of living crinoids, as will be described.

Since in attached forms the most advantageous position for the mouth is on the upper side, whereas in the free sea stars and sea urchins it is on the under side and in the sea cucumbers it is at one end, it becomes confusing to speak of dorsal and ventral surfaces and we will, therefore, use the terms "oral" for the surface on which the mouth is located and "aboral" for the opposite surface. The difference between what may be called the "natural, living" (or physiological) position and the "morphological" position is readily seen in the accompanying diagram if we consider the natural position of a stalked crinoid as also the morphological position (Fig. 26).

All existing echinoderms hatch from the egg as free-swimming ciliated larvæ which are all rather similar to one another and to a variety of worm larvæ, and this fact, together with various adult structural features, has suggested, to most students, that the original ancestors of the phylum were wormlike animals. This view is embodied in the following hypothesis of their evolution, which was first proposed by Bather and is called the "pelmatozoic theory." It explains in a very satisfactory way the manner in which the cystoids, blastoids, and crinoids originated and are related to one another.

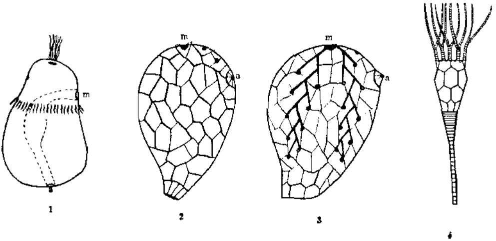


FIG. 27.—Diagrams illustrating the supposed evolution of the Pelmatozoa. (*After Bather.*) 1. The hypothetical Dipleurula. 2. Aristocystites. 3. Fungocystites. 4. Macrocystella: *m*, mouth; *a*, anus.

Starting with a purely imaginary type, modeled after the free-swimming larvæ of the existing echinoderms or those of such a worm as Phoronis or Balanoglossus, we visualize a small pear-shaped soft body with a ganglion at the smaller end probably surmounted with a tuft of long cilia and, perhaps, with one or more bands of shorter cilia around the body, a mouth toward the small end opening into a curved alimentary canal with the anus at the other end—much like a trochosphere. Such an animal we will call a Dipleurula (Fig. 27[1]). To start the Echinoderma phylum, such a free-swimming form need only become attached instead of free. It would become attached, as all known larvæ of this kind do, near the sensory end (which contains the ganglion). As in all attached forms, the mouth would move to the new upper surface which is by far the most advantageous position for a mouth. This would cause a loop to form in the alimentary canal such as is found in all echinoderms and would bring the

mouth in the neighborhood of the anus, as in cystoids, blastoids, and crinoids. The secretion of a plated dermal skeleton would result from the greater need of protection required by an attached, as compared with a mobile, organism—a protection against enemies from which it could no longer flee but also from an environment in which it would no longer be tossed passively about. If we imagine all this to have happened and search the earlier fossil record for some actual fossil which seems to fit the requirements, we find an admirable one in the genus Aristocystites of the Ordovician of Bohemia (Fig. 27[2]). In this, the pear-shaped test of numerous irregular plates is attached directly to the bottom by one end, the mouth at the apex, the anus to one side, and two other openings between the mouth and anus which are interpreted as a water pore and a genital pore. The most vital problem confronting an attached animal is the securing of an adequate supply of food and this is solved in a variety of ways among unrelated invertebrates by some method of setting up currents of water which carry the minute food to the mouth. Getting a suggestion from the way this is done in the crinoids, we can imagine ciliated bands on the upper surface of Aristocystites performing this function in a feeble or primitive way. These incipient food grooves tend to affect the arrangement of the adjacent plates and several well-marked evolutionary trends are discernible among these early forms. First, there is the raising of the form above the bottom by means of a stalk which consists of the lower plates. In Aristocystites it will be noticed that the ring of plates at the base comprises the only regular plates of the whole test except for the little pyramid of plates around the anus. If one can imagine taking the lower part of the Aristocystites test in one's hand and squeezing it so that the viscera are forced into the upper part and the lower part is compressed into a sort of a stalk or stem, one has a good idea of what gradually took place in the early Paleozoic. The longer the stem of an attached organism the greater the radius of its sphere of food supply. Two evolutionary trends are concerned with the food grooves: In the one and less efficient, they radiate as much as possible over the surface of the test. This may be illustrated by Fungocystites—another European Ordovician genus—in which definite food grooves zigzag over the surface of the test from the mouth outward and downward (Fig. 27[3]). At the end of each branch there is a small articular point and there

is no doubt that in life each branch was extended outward into the water by a small, jointed appendage like the brachiole of many genera in which these free branches are preserved.

In the second line the food grooves radiated from the mouth to the edge of the oral surface and were there continued outward and upward in the water. This may be illustrated by Macrocystella, a Cambrian genus and, hence, older than Aristocystites or Fungocystites, thus emphasizing the fact that we are not dealing with the true evolutionary series but merely illustrating theoretical stages by well-preserved but not necessarily related examples (Fig. 27[4]). This second method of increasing the area

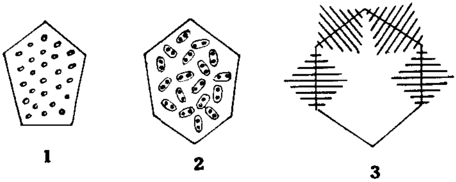


FIG. 28.—Single plates showing the three kinds of pores in the Cystoidea. 1. Simple pores of Aristocystites. 2. Diplopores of Glyptosphærites. 3. Pore rhombs of Echinosphærites.

from which to draw water and its contained food was the more successful for it was perfected in the crinoid class which became dominant in the middle Paleozoic and continued to flourish down to the present, whereas the other method was perfected in the blastoid class and after a fairly successful Paleozoic career became entirely extinct and died out during the Lower Carboniferous.

It is not difficult to picture the evolution of blastoids, edrioasteroids, and crinoids from the cystoids, although we have not discovered the actual stages. The edrioasteroids never developed stalks, and became flattened. The mouth, water pore, and anus remained as in the more primitive cystoids but the food grooves radiated between instead of over the plates of the test. One line remained small and attached by their whole aboral surface and the food grooves were confined to the oral surface which was bounded by a raised border. The other line were more inflated and the aboral surface of attachment was consequently more restricted and the food grooves extended over the edges and on to

the aboral surface. The latter forms frequently became detached and led a free existence, and it is these or something like them that are supposed to have furnished the ancestry of the sea urchins and sea stars. The ancestor of the sea cucumbers among the variety of early forms of echinoderms remains problematical.

CLASS I. CYSTOIDEA

The cystoids have been wholly extinct since the Devonian. They are the oldest and simplest echinoderms. Generally, they are rare fossils, and usually they are imperfectly preserved, having lost both their brachioles and stems. The constituent plates of their test are often not uniform in shape and may be quadrangular, pentagonal, hexagonal, or polygonal; they are united with one another by sutures and during the racial history of the cystoids show a progressive series of changes from those in which the number of plates and their arrangement are entirely irregular to a regular arrangement of a much reduced number of plates.

Aside from the larger openings in the test, such as the mouth, anus, water pore, and genital pore, several or all of the plates are pierced by tiny pores, which are often relied upon in the classification of the different forms. These tiny pores may be arranged singly or in pairs, and when they are in doublets they are called "diplopores." Both the single and the double pores are radial—that is, at right angles to the surface of the plates. Another group have the surface of the plates in certain regions of the test arranged in parallel tangential folds or pierced by parallel tangential canals, half of their extent in one plate and the other half in an adjacent plate—the whole in the form of a lozenge or rhomb. These are called "pore rhombs," and although their exact function is conjectural, they characterize some of the more specialized groups of cystoids.

The jointed appendages or brachioles are absent in the earliest forms and few in number (Figs. 27[2 and 3]) and frequently feebly developed. The earliest forms are stemless, the later stemmed forms usually have short or abbreviated stems, and some are believed to have become detached and to have led a free existence.

Appearing in the record in the early Cambrian, they reached their maximum in the Ordovician and gradually declined to extinction before the close of the Devonian. They show a con-

siderable variety of form and doubtless had a variety of habits, but their evolutionary trends are obscure and the most that can be said is that they failed to solve the problem of adaptation as successfully as some of their descendents which became the founders of the other classes of echinoderms as we recognize them.

CLASS II. EDRIOASTEROIDEA

Test more or less flattened; of an indefinite number of irregular, thin, flexible, united plates; without stalks; attached by the aboral surface or free. A central mouth from which five unbranched food grooves radiate. Food grooves between test plates, floored and roofed by tiny plates (the flooring plates), with pores between them.

These forms, which were formerly included in the preceding class, are never abundant, although they range from the Cambrian to the Lower Carboniferous. They are not only rare fossils but also are frequently poorly preserved.

CLASS III. BLASTOIDEA

Short stemmed, or stemless in certain specialized forms, with a rigid test which, except in the small and primitive Ordovician genera Asteroblastus and Blastoidocrinus, consists of 13 principal plates arranged in three cyles—three basals at the top of the stem, five radials above the basals and at the top alternating with the radials, five deltoids or interradials. Important features are the structure and arrangement of the small plates in the food grooves (ambulacra) and the folds in the test plates adjacent to or underneath the food grooves known as "hydrospires."

The blastoids are an exceedingly interesting group with a variety of forms from the later Ordovician to the Lower Carboniferous, especially familiar to beginners in the form of the excessively abundant Pentremites of the Lower Carboniferous which will be described in some detail.

Pentremites usually occurs in the rocks as relatively small globular or pear-shaped, radially symmetrical tests, that suggest flower buds, and lacking their stems and brachioles (Fig. 29).

At the bottom of the test there are three basal plates, one narrow and two wide ones each of which is made up of two narrow plates which have become united along their adjacent edges. Above the basals there is a zone of five large V-shaped plates

called "radials." The central lanceolate opening in each radial is occupied by the food groove or abulacrum. Alternating with the radials and occupying the points between the oral ends of the ambulacra are five small rhombic plates called "deltoids," making a total of 13 plates to the test. Each ambulacrum in surface view shows a median food groove, which gives off on alternate sides at nearly right angles secondary or branch food grooves which run outward almost to the margins of the abulacrum. The five main food grooves run to the center of the oral surface and empty into the pentamerous mouth. Alternating with the five food grooves around the mouth are five openings called "spiracles." The posterior one of the five is about twice as large as the other four and is a combined spiracle and anal opening. If a specimen is turned over and the aboral view looked at, there is seen in the center the circular attachment of the stem surrounded by the three basal plates of the test and the lower part of the five radials with just the ends of the ambulacra showing. Note that in the oral view the only departure from a perfect radial symmetry is the enlarged anal spiracle opening, and in the aboral view the only departure from a radial symmetry is the three, instead of five basal plates. The ambulacra deserve more detailed study. In any well-preserved specimen it can be seen that each lateral branch from the central food groove ends in a tiny round boss a short distance within the margin and that alternating with these bosses and between them and the margin is a row of holes or pores. If the oral end of a test is ground off in order to see what is underneath the ambu-

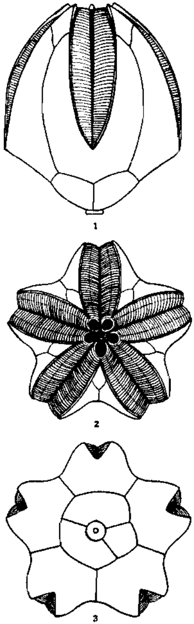


FIG. 29.—Pentremites in side view (1), oral view (2), and aboral view (3).

lacrum, there will be found an arrangement of parts approximately as in the much enlarged figure. Each ambulacrum is seen to consist of a central plate called a "lancet plate" beneath which is a narrower under-lancet plate. On each side of the

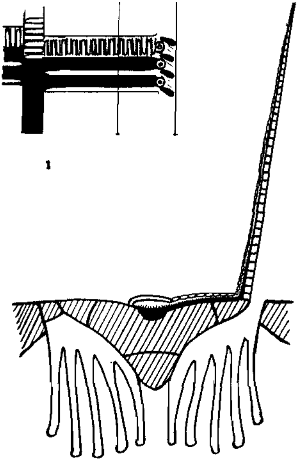


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FIG. 30.—1. Surface view of three lateral food grooves in one-half of an ambulacrum of Pentremites; one with the cover plates closed and two with the cover plates gone (the usual condition in fossils); the facets where the brachioles were attached are shown at the ends of the lateral grooves, and outside these and alternating with them are four of the pores opening into the hydrospires. Much enlarged. 2. Cross-section of an ambulacrum in Pentremites showing the hydrospire folds below; the lancet, underlancet, and side plates above; the central ciliated food groove with its cover is shown in the center of the lancet plate in solid black, and to the right a lateral food groove with its cover plates extending to the end of the brachiole. Much enlarged.

lancet plate is a row of side plates. Usually, the lines formed by the junction of the side plates with the lancet plate can be made out in surface view. The row of tiny bosses is at the outer ends of the side plates. Along the edges of the ambulacrum is a row of small outer side plates between which is the marginal row of

slitlike holes or pores opening into the interior. These open into a passageway extending the whole length of the ambulacrum beneath the edges of the lancet plate and the side plates. From the edges of the bordering radial plate of the test a thin wall of calcite hangs down into the interior. This is arranged in several deep folds and at the inner edge is united to the sides of the under-lancet plate. This passage with its folded floor is called a "hydrospire." Water enters the hydrospire through the marginal pores and flows inward toward the mouth, coming out through the spiracles. Doubtless, in life the hydrospires were covered with a ciliated skin the cilia of which maintained the current, and the function of the hydrospires is supposed to have been respiratory—that is, they enabled the blood to extract oxygen from the sea water.

More completely preserved specimens show that in Pentremites and all other blastoids there were more plates which usually fell away and were lost when the soft parts rotted. First of all, there was a stem of round, cylindrical joints by which the animal was attached. Articulating on each tiny boss at the ends of the lateral branches of the food groove was a slender armlet called a "brachiole" made of minute, calcareous joints. These joints were notched on the inside and in life the branches of the food groove were continued outward to the ends of these hrachioles and were ciliated gutters serving to conduct a food-bearing water current from the ends of the hrachiole to the central food groove of the ambulacrum and thence to the mouth. In order to do this effectively, they had to be closed and this was accomplished by an alternating series of very tiny cover plates. In the enlarged diagram are to be seen two of these branch food grooves with the cover plates gone, as they are in most specimens, and one food groove with the cover plates attached as well as a section of the central groove with its somewhat larger cover plates. In life, a blastoid must have looked much like a brush. The number and arrangement of the ambulacral plates and the character of the hydrospires are important features in distinguishing the different genera of blastoids and in giving a clew to their evolution.

Thus, in the most primitive blastoid, known as Codaster, which makes its first appearance in the Silurian, the hydrospire folds are on the exposed oral surface of the test parallel with the ambulacra but not under them. A line of successive modi-

fications can be traced from Codaster through the gene Phænoschisma and Pentremitidea to Pentremites. A secon evolutionary line starts with the Silurian genus Troostocrin and leads to Metablastus, Eleutherocrinus, and Tricoelocrinu A third evolutionary line starts with the Devonian genus Nucle crinus and gives rise to Schizoblastus, Cryptoblastus, Orb tremites, Mesoblastus, and Heteroblastu Most blastoids have small tests, the large not being bigger than an inch or an inch an a half in diameter and the majority bein much smaller. They are sometimes excee ingly common in limestones formed in cle water from the Silurian to the earlier Low Carboniferous. Specimens of Pentremit occur literally in millions in the earli Mississippian limestones of the Mississip valley but have been found nowhere els Other and earlier genera of blastoids have wide geographical range. None is known t have survived the Paleozoic.

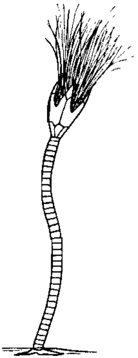


FIG 31.—Restoration of Pentremites showing the root, stem, crown, and brachioles.

CLASS IV. CRINOIDEA

A normal crinoid of simple structure show three principal body regions—a root regio a stem, stalk, or column; and a crown c corona. The crown, which is attached at i aboral pole to the top of the stalk, may b divided into two principal parts—a calyx c theca containing the viscera and, radiating from the rim c equator of the calyx, the five simple or branched arms or brachi The calyx is divided into two regions, the boundary being th place where the arms are given off, separating it into an or region above and inside the arms, commonly called the "tegmen but also sometimes called the "peristome," "vault," or "disk' and the region below the arms, commonly called the "cup" c "dorsal" cup.

In its simplest form the cup consists of two or three rings c alternating plates, five in each ring. Immediately below th arms are five large plates known as "radials." Below th radials are five plates, interradial in position, known as "basals In some crinoids, these constitute the base of the cup to whic

the stem is attached and such crinoids are called "monocyclic." In others, there is an additional ring of plates below the basals and radial in position. These are called "infrabasals" and crinoids, in which infrabasals are present are known as dicyclic. The monocyclic crinoids are supposed to have been derived from the dicyclic by the fusion of the infrabasals with the basals, but it is equally possible that infra basals are new plates added to the monocyclic arrangement.

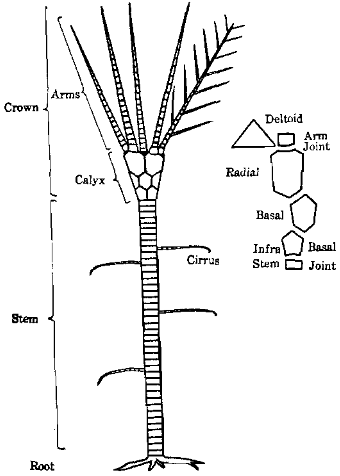


FIG. 32.—Diagram showing the different body regions and hard parts of a simple dicyclic crinoid.

The tegmen part of the calyx in its simplest form consists of five triangular plates alternating with the radials of the cup and known as "oral" or "deltoid" plates. Nearly always, the plating of the tegmen is not so simple but it has incorporated in it modified ambulacral cover plates. The mouth is at the center of the tegmen and the anus is between the edge of the posterior oral and the adjacent corners of the posterior radials. Frequently, near the interior angle of the posterior oral, that

is, immediately behind the mouth, this plate is perforated by a sievelike hydropore which admits water into the interior of the water-circulatory system.

The mouth and the anus commonly are closed by a small, valvular pyramid of small, triangular plates. The arms are the jointed radial prolongations from the radial plates. Each joint is called a "joint," "ossicle," or "brachial." The arms may be simple or repeatedly forked. Through differences of growth in the two branches at a fork, some branches become subordinated to their fellows, resulting in a variety of patterns of unequal branching, a few of which are shown in the accompanying diagram (Fig. 33), and tending toward replacing the many-

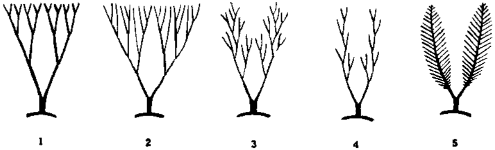


FIG. 33.—Crinoid arms showing the evolution from many forked (1) to once forked with many pinnules (5).

branched arm by two straight branches on which the greatly reduced branches are crowded along either side like the branches of a feather or the teeth of a comb. Such an arm is said to be pinnate, and the branches are called "pinnules" ("armlets," "ramules").

The arm ossicles or joints may be in a single linear series and are termed "uniserial," or they may be in a double alternating series and are termed "biserial." Students are not agreed as to whether the uniserial or biserial is the primitive condition. The explanation given here is that the uniserial is the primitive condition, since the transition from the uniserial to the biserial can be seen at the ends of the arms and extending proximad in both the life history (ontogeny) of certain individuals and in the racial history (phylogeny) of certain extinct genera.

This evolution in form and arrangement is shown in the accompanying diagram (Fig. 34). At the left are shown 4 long joints arranged in a simple series each giving off a single pinnule, so that there are but 4 pinnules in the length of arm shown. The

next figure, with shorter and wider joints, shows 6 pinnules in the same length. In the next figure the articular surfaces have become oblique and there are 7 pinnules in the same length. In the next figure, by very slight changes in form and arrangement, there is a primitive biserial arrangement with the result of increasing the number of pinnules to 12. Finally on the right is seen the completely evolved biserial arrangement with 17 pinnules. Since the function of the pinnules is to collect water and its contained food, any series of adaptive changes in the joints which increases the food-collecting mechanism fourfold is a distinct advantage to the organism which becomes thus modified.

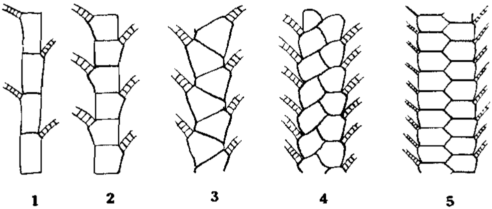


FIG. 34.—Diagram showing the stages in the origin of a biserial many-pinnuled arm (5) from a uniserial, few-pinnuled arm (1).

Consider now how this water- and food-collecting mechanism works. Each pinnule and arm joint is V-or-U shaped, rounded on the outside and with a groove on the side toward the mouth. In this groove are lodged the radial extensions of the blood, water, generative, and nervous systems of the body of the animal in the calyx. These are shown in the accompanying diagram across a single joint (Fig. 35). The whole is covered with a profusely ciliated skin and the action of these cilia keeps the water with its contained food in constant motion toward the mouth. Immediately below the ciliated skin of this food gutter or groove is a nervous cord, below that a blood vessel, below that the water vessel, and, still more deeply buried, the genital cord and other nerve trunks. The whole is roofed over by a series of tiny alternating cover plates which can be raised or lowered. When these cover plates are closed the food groove is a closed canal. When

they are raised water is admitted and the podia or tentacles which serve for both respiration and sensation are extended by increasing the water pressure in the water system. In Fig. 36 are shown four arm joints of a crinoid viewed from the inside. In the lower two joints the cover plates of the food groove have been removed; in the third joint they are shown closed; and in the fourth joint they are raised.

The stem, stalk or column, by which the primitive crinoids were attached was already evolved and inherited by the crinoids from their cystid or

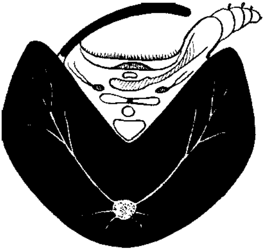


FIG. 35.

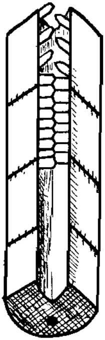


FIG. 36.

FIG. 35.—Section across a single joint of a crinoid arm (soft parts in outline, calcareous parts in solid black). Much enlarged. The cover plate is raised above the ciliated food groove, and a podium (for sensation and respiration) is seen extended at the right. The various radial systems are seen in section below the ciliated surface. Nerves are dotted and the water vessel which operates the podia is obliquely lined.

FIG. 36.—Diagram showing four joints of a crinoid arm from the inside. On the top joint the cover plates of the food groove are raised. On the second joint they are closed, and they are omitted on the lower two joints.

blastid ancestors. It varies enormously in length, some Mesozoic forms having had stems said to be 70 feet in length. The normal length may be said to be from 1 to 3 feet, but in many forms it becomes much abbreviated and these forms may be directly attached by the base, as in Holopus, or entirely free, which is an adaptation seen in numerous forms both in the Paleozoic (Agassizocrinus), Mesozoic (Uintacrinus), Tertiary, and Recent (Comatulids). The stem joints are circular or pentagonal in outline and are pierced by an axial canal which is larger in the earlier and smaller in the later forms. In

many early crinoids the stem ossicles, or "columnals," as they are properly called, are in five alternating series. By slight shifts in their surfaces of contact, as shown in the diagram (Fig. 37), they tend to become arranged in parallel rows and then to coosify to form a single disk-shaped joint. The columnals are not always of the same size. At more or less regular intervals on the stem of the majority of crinoids are larger columnals. These are called "nodals" and the intervening smaller columnals are called "internodals." The jointed appendages of the column, when present, are borne on the nodals. These appendages are called "cirri" and consist of small, calcareous joints called "cirrals." These are pierced by an axial canal which communicates with the axial canal of the stem by radial canals through the nodal. The cirri vary greatly in size, arrangement, and flexibility. They may be singly or in whorls on the nodals. In the majority of Paleozoic forms they are confined to the lower part of the stem. In the order Camerata they are absent except at the base where they constitute the root. Where the cirri are flexible they are used to hold fast to adjacent objects, something like the tendrils of a climbing plant.

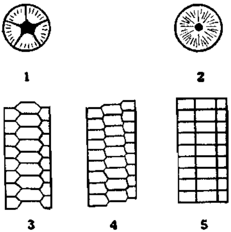


FIG 37.—1. A stem joint of five pieces with a large axial canal. 2. A compound joint with a small axial canal. 3, 4, 5. Showing the gradual transition from alternate to a cyclic arrangement of the stem joints, stages preceding consolidation.

Thus far we have been concerned with rendering the main structural features understandable, which is why a simple crinoid has been described. But most crinoids are not simple and it remains to point out briefly the adaptations that have so modified the foregoing simple type in different directions. There are, of course, an endless number of individual variations and specializations that cannot be mentioned. In general, it can be said that the more important adaptations have to do with increasing the food supply by increasing the length of the stem and of the arms in attached forms, or by the little understood union of the arms by either a leathery or a plated skin; increasing the capacity of the calyx by incorporating the lower brachials in

the cup and the lower ambulacrals in the tegmen; changes in the position of the food grooves on the tegmen, that is, whether they pass over or between or underneath the oral or other tegminal plates; the building up of a sewer-like tube of small plates (the anal chimney) from the anus more effectively to carry off the waste products and prevent any possible fouling of the water and

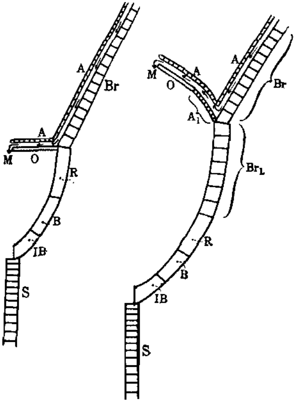


FIG. 38.—Diagrams showing how a simple dicyclic crinoid (left) incorporates arm joints into the calyx and ambulacral plates into the tegmen (right). *S*, stem, *IB*, infrabasal, *B*, basal, *R*, radial, calyx plates. *M*, mouth. *O*, oral plate of tegmen. *A*, ambulacral or cover plates. *Br*, arm joints. Br_1, arm joints incorporated in the calyx. A_1, ambulacrals incorporated in the tegmen. Arrows in the food grooves indicate the water current leading to the mouth.

food supply. In forms that build such sewers new plates are intercalated among the tegminal and calyx plates in the posterior interradial region to accomodate for the necessary enlargement of that area.

Other modifications are concerned with changes in habit, chiefly that of becoming detached, either temporarily or permanently, and leading a drifting life, or replacing the stem by a central aboral plate with cirri which act as holdfasts and at times as feeble crawling organs.

Perhaps the increase in the size of the calyx by utilizing brachials and ambulacrals is hardest to visualize. This may be simplified and rendered understandable by means of the accompanying diagrams (Fig. 38). That on the left shows part of the stem, one arm, and a section of the calyx wall of a simple dicyclic crinoid. If one will imagine the soft parts inserting themselves between the oral and radial, thus forcing them apart, and ascending the food groove, thus forcing the cover plates (ambulacrals) away from the arm joints or brachials so that a certain number of the ambulacrals become incorporated in the tegmen and a certain number of the brachials become incorporated in the cup, as shown in the right-hand diagram, one will have fully grasped the process. Of course, this adaptation in nature was not quite so diagrammatic but involved a certain amount of rearrangement and enlargement of the plates thus utilized to add to the calyx walls, especially of the ambulacral plates thus utilized. Sometimes, the brachials are large enough to allow the lateral edges of those incorporated in the cup to be directly united to one another (*e.g.*, Ichthyocrinus). In others, supplementary interradial plates (interbrachials) are secreted between the brachials that are thus incorporated (*e.g.*, Forbesiocrinus). Moreover, the food grooves do not always retain their position on the roof of the tegmen but may penetrate it at the margin and run beneath it to the central mouth, which is then concealed beneath the vaulted or domed tegmen.

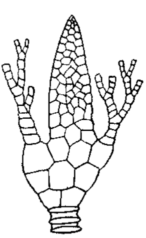


FIG. 39.—Rear view of Parisocrinus (*after Goldring*), showing the top of the stem, the calyx, the lower part of two of the arms, and the anal chimney.

The construction of an anal chimney, while it takes various sizes and forms, may be understood by a single illustration and need not be described in detail (Fig. 39).

As early as the Ordovician, certain attached crinoids either accidentally or voluntarily became permanently or often temporarily detached and after drifting for a longer or shorter period again developed new roots from their distal cirri. Others developed a knob or grapnel-like enlargement at the end of the now free stem which by its weight served as a sea anchor to keep them vertical in the water or to afford a temporary anchorage

when this sea anchor grounded on the bottom. In one genus (Scyphocrinus) this anchor was about the size of a baseball (Camarocrinus, it is called) and is believed to have been due to the growth stimulus of tiny parasitic worms that habitually infested the end of the stem. Still other forms were permanently stemless at maturity, although they were probably temporarily attached when young, and developed a solid bulblike calcareous plate at the aboral pole of sufficient weight to maintain them in an upright position.

In one order (Articulata) its members are habitually stemless and have a single central plate at the aboral pole representing the vanished stem and this supports a whorl of many flexible cirri by means of which they cling to foreign objects or slowly crawl about.

Habits.—Existing crinoids are found between 52 degrees south and 81 degrees north latitude in all oceans—the stalked forms having a narrower range by about 19 degrees of latitude. They are prevailingly gregarious and the vast majority occur in shallow water. As a rule, single species have a limited range and the majority of fossil species appear also to have inhabited shallow waters and had a limited geographical range.

CLASSIFICATION

Crinoids are usually grouped in four orders which will be briefly characterized:

Order 1. Inadunata.—No arm plates incorporated in the calyx. Calyx rigid through having the calyx plates firmly united with one another. Monocylic or dicylic. Mouth sunk below surface of tegmen. Food grooves on the surface of the tegmen. Arms with or without pinnules.

This order includes the simplest crinoids, some of which have no supplementary calyx plates. There are many families, especially in the older Paleozoic. One family survived the Paleozoic and became extinct in the Triassic.

Order 2. Camerata.—Monocylic or dicyclic crinoids which reached their maximum development in the Silurian and Devonian, becoming extinct before the close of the Paleozoic.

In all, except a few Ordovician forms, the plates of the whole calyx (both tegmen and cup) are rigidly united. Arm plates, both brachials and ambulacrals, incorporated in this rigid calyx. Mouth below the tegmen, as are the food grooves in their course from the base of the arms to the mouth. Brachials uniserial or biserial, with pinnules.

The Camerata were highly specialized particularly in the domed tegmen and solid union of all of the plates.

Order 3. Flexibilia.—*Crinoids in which the lower arm plates were incorporated in the calyx by lateral union, by the formation of supplementary plates, or by a leathery skin more or less studded with small plates—but never rigidly.* Tegmen flexible with an exposed mouth and food grooves. Arms uniserial, without pinnules and usually short and stout, as are the stems.

The Flexibilia appear in the Ordovician and are strictly limited to the Paleozoic.

Order 4. Articulata.—Arms freely movable, uniserial and with pinnules. Tegmen leathery studded with very small plates, its mouth and food grooves exposed. Generally radially symmetrical and with anal plates in the cup. Arm plates free or more or less incorporated in the calyx. Stem frequently greatly reduced or wanting except for a modified columnal which is usually enlarged and wholly or partly incorporated at the aboral pole of the calyx.

The Articulata appear in the Triassic and continue down to the present, having about 600 existing species.

CLASS V. STELLEROIDEA

The Stelleroidea, often called the Asterozoa, are stemless free forms with a star-shaped or pentagonal body consisting of a central disk and five or more rays (arms). The mouth is central and on the side usually called the lower, and the anus is on the aboral (upper surface). The skin is leathery and contains loosely united calcareous plates which are frequently tuberculated or spiny. Stelleroids are found as far back as the Ordovician in shallow-water sediments and are usually preserved as casts in muddy rocks, so that they are normally uncommon fossils and difficult to study. A modern sea star (usually called "starfish") turned on its back has all its principal organs and parts corresponding with those of a crinoid.

The class is usually divided into three subclasses: the Asteroidea or sea stars; the extinct Auluroidea; and the Ophiuroidea or serpent, brittle, sand and basket stars. Each of these will be considered separately.

Subclass 1. Asteroidea

The Asteroidea have the arms invariably simple and containing radial extensions from the organs of the central disk. The skeletal plates are continuous, overlapping, or reticulately joined and are covered by a leathery skin through which the spines protrude. The aboral surface shows a central or subcentral anus and one or more madreporites in one or more

interradial areas. Tiny, soft, saclike protrusions into the water from between the plates are known as "papulæ" and are respiratory in function.

From the central mouth there radiate as many broad, deep furrows as there are arms, and these furrows correspond to the food grooves of the crinoids but show modified structures and have modified functions. The roof (or floor) of this furrow consists of two rows of transversally elongated, rafter-like plates, known as "ambulacrals," and their inner ends are held together by muscles. These rafters, or ambulacrals, are end to end in recent sea stars but are frequently alternately arranged in Paleozoic forms. They are excavated on the sides where they join one another, thus forming a series of holes or pores, and it is through these pores that the podia or tube feet protrude.

By means of these tube feet, or podia, the animal crawls. They are a part of what is called the "water-vascular system" and are operated in the following manner: Sea water enters from the outside through the madreporite and is conveyed by a canal known as the "stone canal" to a ringlike vessel around the gullet. From this ring a radial water vessel runs along the center of each ambulacrum. This radial water vessel gives off as many right and left branches as there are ambulacral plates. Inside the plates these branches have bulblike enlargements known as "ampullæ," and outside the plates they have a flexible axis with a sucker-like end. They are small in size but make up for their small size by their great numbers so that a sea star can pull open an oyster or other bivalve on which it feeds.

The more or less inclined ambulacrals have their outer ends resting against plates called "adambulacrals" and these may be bounded by intermediate plates or a row of larger infra- or supra-marginal plates, those on the aboral surface being simply known as "dorsals" or "aborals." Those sea stars which have a conspicuous row of plates along the margins of the arms are classed as Phanerozonia (Fig. 40[3]) and those in which they are not enlarged or conspicuous are classed as Cryptozonia (Fig. 40[4]), but the classification of the whole subclass is in a very unsatisfactory condition.

The simplest and earliest asteroid is called Hudsonaster and is a small form found in the middle and upper Ordovician. The plates of the aboral part of the disk are very similar to those of a modern baby sea star before the arms have grown out.

The general course of evolution among the sea stars consist in a progressive increase in size: a relative increase in size of the central disk, by its extension outward at the expense of the proximal parts of the arms; elongation of the arms; and increase in capacity of the body as a whole—easily accomplished by increasing the number of plates. These changes in various lines of descent takes place relatively slowly and the whole group seems to have been fairly stable from the Paleozoic to the present.

SUBCLASS 2. AULOROIDEA

This is an extinct group supposedly derived from Asteroid ancestors, which appeared in the Ordovician and became extinct before the close of the Paleozoic. Members resemble the Ophiuroidea in general form, differing from the Asteroidea in the sharp boundary between the central disk and the relatively slender and elongated arms. Rays apparently always five in number and simple (not branched). Ambulacral furrows open (Fig. 40[2]).

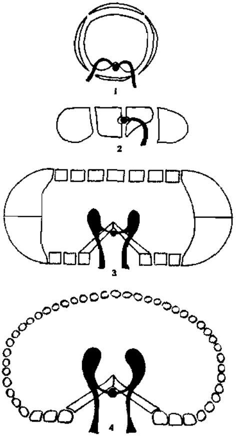


FIG. 40.—Cross-sections of stelleroid arms in the different groups. 1. An ophiurian. 2. An auluroid. 3. A phanerozoniate asteroid. 4. A cryptozoniate asteroid. (The plates are in outline and the radial water vessel and podia, or tube feet, are in solid black.)

SUBCLASS 3. OPHIUROIDEA

These were probably derived from the Auloroidea in the Devonian although not known earlier than the Carboniferous, from which time they extend to the present. The disk is sharply separated from the long, flexible, frequently branched arms. Viscera confined to the disk. The madreporite is on the oral surface. The arms usually lack ambulacral furrows and consist of a central series of articulating plates (the vertebral ossicles) formed by fusion of the ambulacral plates, surrounded by four rows of arm plates—an upper and lower and two series of side

plates (Fig. 40[1]). They usually wriggle instead of crawl and the tube feet, hence, have lost their crawling function and serve for respiration.

CLASS V. ECHINOIDEA

This class comprises forms without any trace of stem or arms; globular or diskoidal in form. A compact and well-marked group whose distinctness has been recognized since the days of Aristotle. The Echinoids, or sea urchins, are exclusively marine and more or less gregarious. The recent forms, numbering 500 to 600 species, are widely distributed in all seas at all depths, the majority at moderate depths. Like the sea stars they are all bottom dwellers. They appear in the geological record during the Ordovician and are abundant as fossils from the Devonian onward. Their classification depends largely upon the skeletal structures or upon features readily inferred from the skeleton. Consequently, they can be determined with precision. This and their varied habits make them exceedingly useful to the geologist.

Some burrow in sand, others bore in rocks, some live in tidal pools or cling to rocks within tidal limits, others crawl over or lie partially buried on soft bottoms. Some feed on algæ, others live on organic mud, and others are carnivorous. In some, the young develop directly; in others, the early stages are unlike their parents.

The test of a sea urchin consists of three systems of plates—a circular area around the mouth covered with a leathery skin which is more or less studded with small plates—the peristome; at the opposite pole from the mouth in the radially symmetrical forms is the anus, surrounded by a circular system of plates called the "apical" or "oculogenital system"; the region between the peristome and the apical system, which constitutes the bulk of the test and is the part commonly preserved in fossils is called the "corona." The corona invariably consists of ten meridional areas of plates, five ambulacral areas alternating with five interambulacral areas.

In post-Paleozoic forms the majority of sea urchins have 2 alternating rows of plates in each ambulacral and interambulacral area, the ambulacrals being perforated or pored and the interambulacrals imperforate. In modern forms the plates are rigidly united but in certain fossil forms their edges are beveled, thus giving them a certain degree of flexibility. In all Recent

and the majority of fossil forms each ambulacral area is bilaterally symmetrical and consists of 2 alternating rows of plates, the inner edges uniting in a median zigzag suture. In some Paleozoic genera there are more than 2 rows of ambulacrals and there may be as many as 20 rows (Fig. 41). All ambulacral plates are pored, typically near their outer margins. These pores are in pairs in all but a few forms. When the pore pairs lie directly one above the other in a single meridional line (*e.g.*, Cidaris,

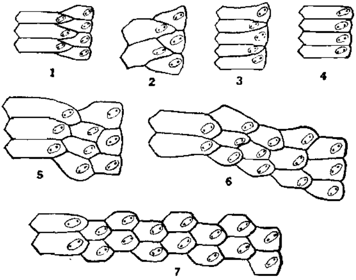


FIG. 41.—Right halves of ambulacra in various Lower Carboniferous genera to show changes in plate arrangement with the widening of the ambulacral areas. (*After Jackson.*) 1. Lovenechinus with 4 rows of fairly regular plates. 2. Another Lovenechinus in which the plates are less definite and regular. 3. Maccoya in which the alternate plates scarcely reach the ambulacral border. 4. Palæechinus with but 2 rows of plates in each ambulacrum. 5. Melonechinus with incipient 6 rows of plates. 6. Another Melonechinus with 10 rows of plates. 7. Lepidesthes with 16 rows of ambulacrals.

Fig. 42[1]) they are said to be uniserial, the number of ambulacrals in a column will be found to be numerous, and they will be much wider than they are high. When the pore pairs are placed so that 2 rows can be made out on each margin of an ambulacral area they are said to be biserial (*e.g.*, Diadema Fig. 42[2]). Each plate will be seen to be higher than in the preceding case and not simple but compound. Forms with more than 2 rows of pore pairs along each margin of an ambulacral area are said to be polyserial, and the kind and arrangement of the plates which go to make a compound plate are of great systematic importance (Fig. 42).

Thus, plates which extend from the median suture to the margin, that is, halfway across the area, are called "primaries," those that are shorter are called "demi-plates." These shorter plates typically extend from the margin part way inward. If neither end reaches either the margin or the median suture they are said to be isolated, and if they extend from the median suture but part way to the margin they are said to be occluded.

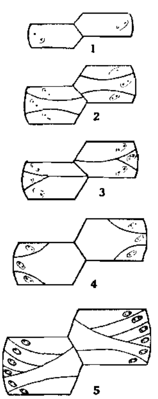


FIG. 42.—Pairs of echinoid ambulacral plates. 1. Cidaroid. Simple plates forming one row of pore pairs near the margins. 2. Diademoid. Compound plates consisting of three primaries, forming two rows of pore pairs near the margins. 3. Echinoid. Compound plates consisting of two primaries and a demiplate, forming two rows of pore pairs near the margins. 4. Arbacioid. Compound plates consisting of one primary and two demiplates, forming two rows of pore pairs near the margins. 5. Cyphosomoid. Compound plates of three primaries and three demiplates forming several rows of pore pairs near the margins.

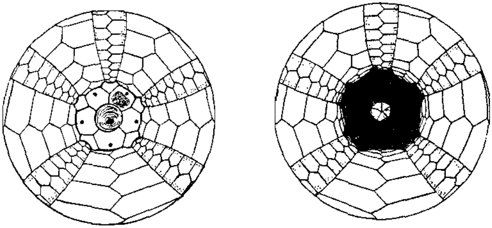
In all evolved forms of radially symmetrical echinoids the ambulacral plates are likely to consist of several coalesced plates, and the number and character of these are of great importance. If they consist of two united primaries they are known as "dyads"; if of three primaries, triads or diademoid (Fig. 42²); if of two primaries and a demi they are echinoid (Fig. 42³); if of one primary and two demis they are arbacioid (Fig. 42¹); if of two or more primaries and two or more demis they are cyphosomoid (Fig. 42⁵).

When the ambulacral areas broaden conspicuously toward the equator of the test they are said to be petaloid and each may be called a "petal."

The interambulacral areas normally consist of 2 rows of plates which are always simple and not compound and usually much fewer in number than the ambulacral plates. In forms in which the ambulacrals are narrow the interambulacrals will be wide, and *vice versa*, and some extinct forms have as many as 14 rows of interambulacral plates in each interambulacral area, and in one group of very ancient forms (Bothriocidarids) there is but a single row of interambulacrals in each area. In the radially symmetrical echinoids all the ambulacral and interambulacral areas are essentially alike (Fig. 43).

In those which are elongated and bilaterally symmetrical the anterior ambulacrum and the posterior interambulacrum often differ conspicuously from the others.

The apical or oculogenital system at the aboral pole of the test consists ordinarily of two alternating rings of five plates each, surrounding the anus—five genitals interradial in position with large pores for the extrusion of the sexual products and five oculars radial in position and standing at the head of the ambulacral areas. The anterior right genital is often enlarged



1 2

FIG. 43.—A regular endocyclic echinoid test in aboral (1) and oral (2) view. In the aboral view the periproct with the anus is in the center surrounded by the the five genitals (pored) and five oculars of the apical system. The anterior right genital is perforated by the madreporite. Outside the apical system are seen the five symmetrical radial (ambulacral) and interradial (interambulacral) areas of the corona. In the oral view the jaws of Aristotle's lantern are seen in the center of the dark peristome which is surrounded by the coronal plates.

and normally contains the madreporite which admits the sea water to the water system. When the arrangement is like that shown in the diagram the oculars are said to be exsert. If one or more oculars wedge between the adjacent genitals and reach the anal border such are said to be insert. In some forms the genitals may fuse into a single pentagonal plate and often the posterior genital pore will be absent. In the bilateral echinoids in which the anus is not in the apical system but has moved backward, the apical system may be compact or may be elongated as shown in the diagram (Fig. 44).

The peristome, which surrounds the mouth, is on the lower side of the test. It is central in position in the radially symmetrical forms and may be in front of the center in bilaterally sym-

metrical forms. It may be leathery and without plates (Clypeasterids) or more or less plated with ambulacrals only or with some of both kinds. In all except one group, which feeds on organic mud (Spatangoids), the mouth is provided with powerful jaws known as "Aristotle's lantern," since they were discovered by this ancient philosopher. The lantern is a large conical affair with the point downward and consists of five principal parts made up of a number of accessory pieces and

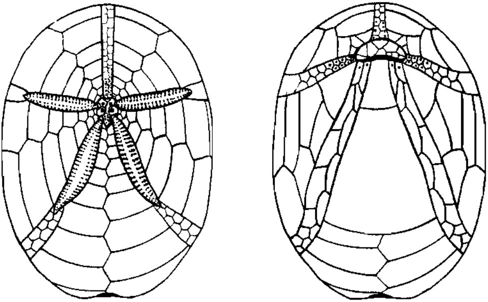


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FIG. 44.—An irregular or exocyclic echinoid test in aboral (1) and oral (2) view. In the aboral view the apical system is slightly in front of the center and the anus has migrated from the apical system and is situated at the hinder margin of the test in the posterior interradial area. Four of the ambulacra are petaloid and the anterior one is linear. In the oral view the peristome is reniform and it has moved forward from the center; the anterior ambulacra have lost some and the posterior pair nearly all of their pores.

operated by powerful muscles which are attached to the basal margin of the corona. These jaws are seldom found fossil.

The coronal surface of the sea-urchins' test is never smooth but is more or less covered with tubercles which in life bear spines of various kinds and degrees of development. In life, also, the whole outer surface and most of the spines are covered by a living ciliated skin, so that the test is, in a sense, an internal skeleton.

In some groups the spines are much reduced and this is especially true of the bilaterally symmetrical forms. They are particularly well differentiated, however, in the radially symmetrical

forms where they and the tubercules on which they are articulated are of three sizes known as primary, secondary, and miliary. Consequently, in life all sea urchins bristle with spines which serve for sensation, protection, and locomotion. The primary spines and the tubercules which bear them are large (Fig. 45). The spine has an articular base and a shaft. The tubercule consists of a central ball-like boss (the mamelon) which may be solid or have a central perforation. Around the boss is a smooth ring (scrobicule) and there may be an outer granular ring (scrobicular circle). The diagram will make clear the arrangement. At maturity the ciliated skin frequently wears off the distal part of the primary spines. The secondary spines and tubercules are like the primary but smaller and retain their ciliated skin through life and carry tactile hairs at their tips. In the radially symmetrical sea urchins both the ambulacral and interambulacral plates carry primaries. The secondaries surround the primaries and the anal and genital apertures like a palisade.

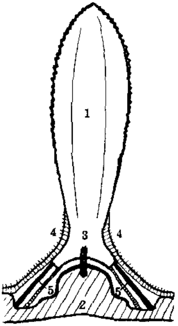

Fig. 45.—Section of a primary spine and tubercle of a regular echinoid. 1. The spine. 2. The tubercle. 3. Central attachment in the perforate types. 4. The ciliated epidermis of the outside of the test. 5. The A-tent-like muscle and ligament which move the spine.

The miliary tubercles are very small and unspecialized and in life carry flexible appendages known as "pedicellariæ."

The spines show many interesting modifications in the different groups. Since their attachment to the test is muscular they fall away after death and, consequently, are almost always found detached in fossils.

The echinoids are usually divided into seven orders. They may, however, be roughly separated into two major types—those which are circular in outline with mouth and anus at opposite poles and are called "regular" or "endocyclic" and those in which the outline is more or less elliptical or heart shaped and in which the mouth may be forward of the center and the anus always back of the center. These are called irregular or exocyclic and are pronouncedly bilateral instead of radially symmetrical.

The most ancient known sea urchin is Bothriocidaris of the Ordovician, which is considered to represent an independent order (Bothriocidaroida). It has an almost spherical test, one row of interambulacral plates in each area and two rows of ambulacral plates in each area, each ambulacral plate with a single pore pair.

A Silurian genus (Palæodiscus) represents a second order (Echinocystoida) in which the interambulacral plates are irregular in shape and the anus lies behind the aboral pole—both features suggesting a cystidean relationship. The majority of the Paleozoic echinoids belong to an order known as the Perischœchinoida which is first found in the Silurian, reaches its zenith in the Carboniferous, and is not known from post-Paleozoic rocks. In this order the few forms in which the jaws are preserved show them to have been simpler than in modern adult forms; the corona, which is the part most frequently preserved, varies widely in the number of rows of plates in the ambulacral and interambulacral areas and the edges of the plates are often beveled, thus allowing some flexibility to the test.

The peristomial margin of the corona is not inflected and thickened to form what is called the "perignathic girdle," which is present in later echinoids and to which the lantern muscles are attached. The peristomial skin is covered with interambulacral and a few accessory plates; and in the apical system the ocular plates are usually insert.

Among the four remaining orders only one—the Cidaroida—is represented in the Paleozoic, possible in the Devonian, certainly in the Carboniferous. It appears to have descended from an ancestor much like Bothriocidaris of the Ordovician.

The cidaroids have evolved slowly down to the present, the changes being chiefly the formation of a partial perignathic girdle at the bases of the ambulacral areas and an increase in the size of the tubercles. In the early Mesozoic they appear to have given rise to the diademoid type (order Centrechinoida) which evolved more rapidly and probably gave rise to the remaining two orders. In the Centrechinoida, the perignathic girdle involves the base of the interambulacral as well as the ambulacral areas and a crowding of the basal plates immediately above the girdle. The ambulacral areas became straight and widened and the plates became compound and consisted of from two to ten elements, each with its pore pair. This is a large and highly diversified group in the later Mesozoic and Recent seas, and only 2 of the 12 families have become extinct.

The order Exocycloida probably arose by modification from some form in the preceding order, possibly some arbacioid type. It is characterized usually by the elongation of the test (irregular or exocyclic) and the assumption of bilateral symmetry, a relative reduction in the size of the apical system and peristomial area. Frequently, the mouth moves forward and in one suborder the jaws have disappeared. The anus moves backward outside the apical system. The spines are less massive than in the regular echinoids and may be absent from certain plates. The tube feet on the upper surface of the test become modified for respiration with a widening of the upper part of each ambulacrum to form a petal, the widening of the space between the individual pores of a pair, and an elongation of the outer pore to form a slit. The pores frequently disappear below the petals to reappear more or less on the ambulacrals as they approach the mouth. The podia are, hence, partly or wholly absent from the oral surface and the function of locomotion—their normal function—is taken over by the spines which pole the animal along as though it were on innumerable stilts. The Exocycloida are prevailingly bottom forms and may be greatly depressed, as in the sand dollars. They are the most modified (or specialized) of the whole class and are exceedingly common from the Jurassic to the Recent. Of the ten families recognized, only one is extinct.

The remaining order, Plesiocidaroida, is based upon a single Triassic form of very small size, which has a relatively large apical system and three rows of interambulacral plates in each area. It may be a relatively primitive or a highly aberrant type.

CLASS VII. HOLOTHUROIDEA

The sea cucumbers differ from other echinoderms in their wormlike bodies, and only by their anatomy are their relations to the other classes clear. Their skins are leathery and there is no calcareous test. The only trace of skeletal elements is usually minute, dissociated, spherical, anchor-shaped or wheel-shaped calcareous spicules. Their geological history rests upon impressions of the body preserved in fine-grained muds, of which some rather convincing examples have been found as early as the middle Cambrian, and by fossil spicules sparsely scattered through the geological column. Holothurians are of no stratigraphic importance and have but a minor interest for the average paleontologist.

CHAPTER VII

BRYOZOA

The Bryozoa (the name means "moss animals" and is not very appropriate) are tiny animals found sparingly in fresh waters and widespread and abundant in marine waters which are not too muddy. Their fossil remains are found in great variety in the sediments of ancient seas since the older Paleozoic. They were named Bryozoa by Ehrenberg in Germany, in 1831, and a year before were christened Polyzoa by Thompson in England, where that term is used in preference to Bryozoa.

With scarcely an exception, a sexually developed free-swimming larva becomes attached to some foreign object—seaweed, shell, rock, driftwood—and by repeated budding forms a colony of many individuals. This colony may form a delicate and often beautiful encrustation the recent forms of which suggested the popular term of "sea mats" for them; or many-layered encrustations may result in the building up of globular, nodular, or irregular masses; or the budding may result in frondlike lacework, or branching forms. As a rule, the general shape of a colony has but slight bearing on the relationships of the tiny animals of which they are composed.

Some of these colonies resemble certain corals or hydrozoans superficially, but the animals themselves are much more complexly organized in having a distinct body cavity, a complete alimentary canal, a relatively elaborate nervous system, respiratory tentacles, and relatively elaborate arrangements for incubating their eggs.

Each individual of a colony is a zooid or polypide and consists essentially of a saclike body enclosing a body cavity in which a U-shaped alimentary canal is suspended. The outer surface secretes a horny or calcareous wall (the zooecium or oecium). At the front or upper end of the body there is a row of delicate, fleshy, ciliated tentacles arranged in a ring or circle and enclosing both the mouth and anus (Endoprocta) or the mouth only (Ectoprocta). Since only the latter group is found fossil and the

relationship of the two to one another is not fully understood, the Endoprocta will not be discussed.

When the trochosphere-like larva hatches, it swims about by means of cilia for a few hours before attaching itself. It then undergoes a transformation the exact nature of which is obscure and the apical part develops into a zooid. The skeleton of this first zooid is known as an "ancestrula" and from this by successive budding the remaining members of the colony are produced, maintaining a living connection with one another through openings (communication pores, parietal pores, or septulæ) in the zooecial walls. Both kinds of sex organs are usually present in a single individual and the fertilized egg cells pass to a brood chamber for hatching. This receptacle may be a modified zooecium or an inflation of the front wall. Much use is made of this feature in systematic work and a variety of terms have been suggested for its different forms. The name "ovicell" is a good general term.

The Bryozoa are all aquatic and mostly marine and their history extends from the early Paleozoic to the Present. The classification of these small forms is not fully understood. The relations of the two classes Ectoprocta and Endoprocta to one another are obscure. The majority of the known forms, both recent and fossil, belong to the class Ectoprocta characterized by having the anal opening outside the tentacles. This class is divided into two unequal groups the smaller of which—the Phylactolæmata—is confined to fresh water and in which the body walls remain muscular and no skeleton is secreted, and the tentacles are arranged in the form of a crescent or horseshoe. Since hard parts are lacking members of this subclass are not found fossil.

The second and larger subclass—the Gymnolæmata—have the tentacles arranged in a ring around the mouth, the body walls are not muscular, but secrete a calcareous or a partly calcareous and partly horny dwelling. They are almost wholly marine and have furnished practically all of the known fossil forms. They are usually grouped in five orders, each of which will be briefly described.

Cyclostomata

The Cyclostomata, probably the most primitive order, have simple, cylindrical or tubular zooecia, with thin, porous walls

without cross-partitions, round apertures not ornamented or contracted, and without lids (opercula). Ovicells when present are enlarged zooecia or inflations of the surface. The group appears in the Ordovician and becomes greatly diversified during the Ordovician and Silurian, the form of the colony varying from uniserial branching to massive forms. They diminish in abundance in the later Paleozoic and early Mesozoic and undergo a

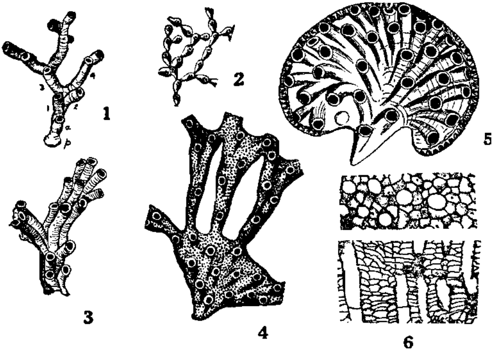

FIG. 46.—Views of cyclostomatous Bryozoan. 1. Stomatopora from the Middle Jurassic, showing protœcium (p), ancestrula (a), and 1, 2, 3, 4, buds, five times life size. 2. Corynotrypa from the Ordovician, six times life size. 3. Entalophora from the Upper Cretaceous, eight times life size. 4. Proboscina from the Ordovician, twelve times life size. 5. Berenicea from the Jurassic, seven times life size. 6. Transverse and vertical sections of Cyclotrypa from the Devonian, fourteen times life size.

renewal of evolutionary activity in the Jurassic and Cretaceous, declining in the later Tertiary to only about 100 existing species.

The group is not entirely understood, the older naturalists having based species on such unreliable features as the form of the colony. The character of the ovicells seems to be of more importance, as are also the features of the earliest zooecium of the colony. In simpler uniserial forms, such as Stomatopora or Corynotrypa, the first zooecium of the colony (ancestrula) is small and tubular with a bulbous dilation at one end (the protoecium) secreted by the larva which started the colony. From divergently branching, the angles of divergence decrease

until the proximal parts are united with their fellows and eventually the whole colony may become so united that new zoids bud from the proximal end of their parents as in Ceramopora or Fistulipora. Smaller accessory tubes may develop on the sides of the zooecia and these may be closed or open and appear to have been uninhabited. These tubules and the various kinds of pores developed all receive special names (firmatopores, tergopores, dactylethræ, cancelli, vacuoles, mesopores) but their functions are unknown and their consideration may well be omitted.

Ctenostomata

The order Ctenostomata is insignificantly represented from the Ordovician to the Present and is very imperfectly known. The zooecia are not calcified although the stems may be partially so and the recent forms have terminal pores with a setose lid. Ovicells are wanting and the fossil forms which are sparingly found at all geological horizons are recognized by the partially or wholly excavated cavities that these animals left in the brachiopod or other shells which they encrusted or in which they ramified.

Trepostomata

The Trepostomata are a wholly extinct order which attained their maximum development in the early Paleozoic. They dwindled greatly in the later Paleozoic and students differ as to whether or not they were present in the Mesozoic. They appear to be wholly Paleozoic and the Mesozoic forms which resemble them have porous walls and probably belong to the Cyclostomata. The skeletons were always calcareous and formed masses of considerable size up to a foot or more in height, made up of long, united, prismatic or cylindrical tubes with terminal openings. Each individual zooecium is a long tube of many stories, each floor called a "tabulium" or "diaphragm" or "cystiphragm" successively inhabited by generations of zooids. The earlier and later parts of these tubes differ, principally in the thickness of the walls, the earlier being much thinner. Hence, the name of the order from the Greek *trepos* meaning "changed." The individual tubes may be in close contact with one another or separated to a greater or lesser degree by an intermediate packing of aborted zooecia and tubular spines, thus

greatly resembling in minature such corals as Favosites or Heliolites with which they have frequently been confused. Their early growth stages show conclusively that they are Bryozoa.

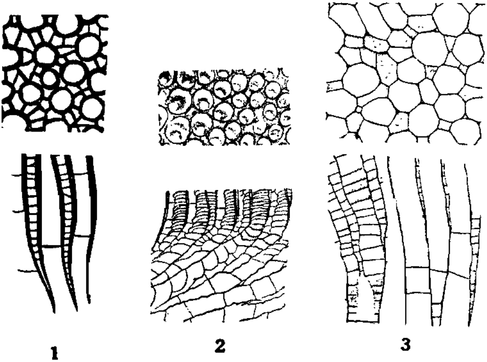

FIG. 47.—Views of trepostomatous bryozoan from the Ordovician in transverse (above) and vertical (below) sections. 1. Hallopora, twenty times life size. 2. Homotrypa, fifteen times life size. 3. Diplotrypa, fourteen times life size.

CRYPTOSTOMATA

The Cryptostomata are almost as abundant and important in the Ordovician and Silurian as are the Trepostomata. Unlike the latter, they continued in but slightly diminished abundance until toward the close of the Paleozoic but are unknown in later rocks. The zooecia are usually short, but some are ramose and have long, thin-walled, prismatic tubes with or without partitions, precisely as in the ramose Trepostomata and Cyclostomata. Their outstanding feature is the external deposit of calcareous matter so that the aperture becomes hidden at the bottom of a tubular vestibule (hence the name, from the Greek *cryptos*, meaning "hidden"). In some of their features the Cryptostomata appear to have been the Paleozoic ancestors of the Cheilostomata, from which they differ in lacking ovicells or appendicular processes, and in the frontal deposits of calcareous

matter. Although the colonies may be branched and consist of long, tubular zooecia, they may also be lacelike or encrusting; more typically, they consist of two short layers of zooecia growing back to back in erect, grasslike, ribbon-like, or fan-shaped branched or unbranched expansions.

FIG. 48.—Diagram of a vertical section of a branch of a Cryptostomatous bryozoan.

CHEILOSTOMATA

The order Cheilostomata represents the modern and most specialized of the Bryozoa. Derived from Paleozoic Cyclostomata or Cryptostomata, they make their first appearance in the geological record during the Jurassic and become very prominent by Upper Cretaceous time. They are the dominant Bryozoa in Cenozoic and Recent seas. Zooecia oval, urn shaped, rectangular, or hexagonal, usually closely spaced side by side. Apertures toward the front end smaller than the diameter of the zooecium, in life closed by a movable horny lid. Eggs commonly matured in external ovicells. Appendicular organs frequently present.

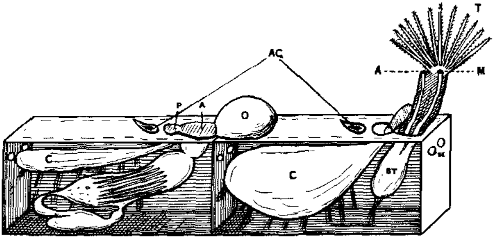

FIG. 49.—Diagram of a Cheilostomatus bryozoan showing the animal withdrawn and the lid closed on the left; the lid open, and the compensating sac expanded and the polyp protruding on the right. (*After Bassler.*) *C*, compensating sac. *O*, ovicell. *A*, *P*, anterior and posterior parts of the lid. *T*, tentacles. *M*, mouth. *A*, anus. *AC*, avicularia. *St*, stomach. *Se*, septulæ or communicating pores between the zooecia.

Not all have a calcified zooecium; in the family Flustridæ it is horny and flexible, whereas in the family Membraniporidæ the front wall is more or less uncalcified. The ovicells are normally external, blister-like cavities in front of the apertures. The

appendicular organs are of two kinds known as "avicularia" and "vibracula." An avicularium is a modified zooecium, the apertural margin and operculum being shaped like a bird's head and snapping against one another like a pair of jaws. They are operated by powerful muscles and may be articulated to, or immovably fixed on, the outer wall. Vibracula are flexible, bristle-like appendages generally set in the hollowed summit of a surface elevation or blunt spine. Neither avicularia nor vibracula are fossilized, but their former presence in fossils is sometimes indicated by the scars where they were attached. Their functions are not certainly known (Fig. 49).

A feature of special interest in this order is the development of a hydrostatic apparatus of which the chief part is the compensating sac. Those with one are grouped in the suborder Ascophora, and its external pore is called an "ascopore." Those lacking this apparatus constitute the suborder Anasca.

CHAPTER VIII

BRACHIOPODA

The Brachiopoda, formerly grouped with the Bryozoa and primitive Chordata into a subkingdom termed the Molluscoidea, are best considered as an independent phylum, derived from wormlike ancestors in pre-Cambrian time.

Brachiopoda are, and always have been, marine animals, with a shell of two pieces—dorsal and ventral. They are nearly all attached to the bottom or to some foreign object in a variety of ways, usually by a posterior prolongation of the body known as a "pedicle" (peduncle or stalk). They never multiply by budding or form colonies, although they are gregarious—apparently because the free-swimming larvæ which hatch from their eggs are poor swimmers and remain free only a short time, so that the majority attach themselves not far away from their parents. The shell is a cuticular structure secreted by the ectoderm and consists of an organic base made rigid by deposits of calcium carbonate or calcium phosphate. The two valves are each symmetrical but unlike, the dorsal valve being usually shorter and shallower than the ventral. The shells differ fundamentally from those of a bivalved mollusk in structure, in the methods of opening and closing, and, more obviously, in being dorsal and ventral instead of right and left, in being unlike instead of like one another, and in being symmetrical instead of unsymmetrical.

The animal which lives in the brachiopod shell is also totally unlike a mollusk. The valves are lined by a mantle the free edges of which frequently are beset with horny bristles. Midway between the front and back of the shell, the inner surface of the mantle sends an oblique, curtain-like partition across the cavity of the shell which divides it into a front part known as the "mantle" or "brachial cavity" and a hinder part containing the visceral cavity—or body proper. In the median part of this partition wall is the mouth which heads backward and upward into the stomach into which empty the so-called "livers." The stomach narrows into a simple intestine which may be without

an outlet (in the group known as the Articulata) or may bend back to an anal opening either below (Crania) or at the right of the mouth (Lingula, Discinisca). This last feature in the two genera mentioned is the sole departure from complete bilateral symmetry in either the hard or the soft parts of the brachiopod. Above the stomach is the small, contractile heart. On either side of the intestine is a nephridium or kidney, shaped like a trumpet, the large ends opening into the body cavity and the small ends opening into the brachial cavity on each side and below the mouth. They serve both for excretion and as genital

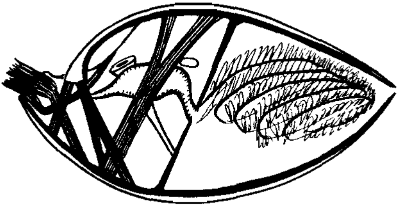

FIG. 50.—Median section of a brachiopod in its shell. Front at the right, hind end with pedicle at the left. The mantle lining the shell and its internal growth dividing the interior into an anterior brachial and a posterior visceral cavity are in solid black. The coiled lophophore is seen in the brachial cavity. The mouth is in the center of the mantle curtain or diaphragm and leads into a closed alimentary tract. Above the mouth is the ellipsoidal heart. The trumpet-shaped organ back of the stomach is one of the nephridia or kidneys. The muscles which move the valves on the pedicle, and which open and close them, are lined.

ducts. The reproductive organs lie in the lining of the body cavity, two dorsal and two ventral, and their products are discharged directly into the body cavity, finding their way out through the nephridia. Sometimes both sexes are represented in an individual (Thecidium). In other genera (Terebratulina, Discinisca) the sexes are distinct. Brachiopods are so largely extinct that we cannot generalize on this point, but it seems probable that distinct sexes were the rule.

The brachial cavity contains a pair of soft, coiled appendages commonly called the "arms," "brachia," or "lophophore." These take their origin on either side of the central mouth, serve for gathering food and for respiration, and are often capable of being extended beyond the shell. Their structure is most inter-

esting. Figure 51[1] shows the inside of the dorsal valve of a Rhynchonella with the central mouth and the coiled arms like a giant mustachio. One is coiled within the shell, the other is extended beyond it. The cross-section of an arm shows how they work (Fig. 51[2]). They are slender, cartilaginous affairs carrying muscles, nerves, and blood vessels. The upper edge is fringed with long, closely spaced tentacles and the front margin has a flangelike lip. Between the tentacles and the lip is a gutter. The tentacles can be bent over so that their tips touch the lip, thus virtually forming a closed tube and, as the whole is profusely

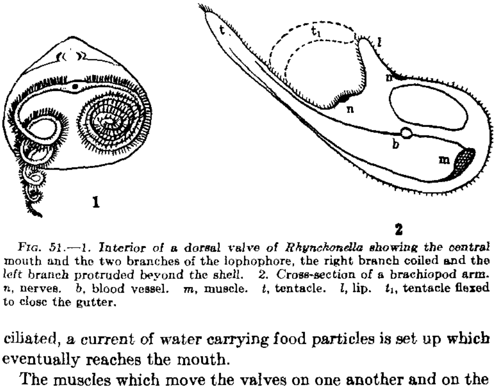

Fig. 51.—1. Interior of a dorsal valve of Rhynchonella showing the central mouth and the two branches of the lophophore, the right branch coiled and the left branch protruded beyond the shell. 2. Cross-section of a brachiopod arm. *n*, nerves. *b*, blood vessel. *m*, muscle. *t*, tentacle. *l*, lip. t_1, tentacle flexed to close the gutter.

ciliated, a current of water carrying food particles is set up which eventually reaches the mouth.

The muscles which move the valves on one another and on the pedicle are quite elaborate and the mechanism is totally different from that of the bivalved mollusks. There is, also, considerable difference in the musculature between the two main divisions of the Brachiopoda—the Articulata and the Inarticulata, or those in which a hinge is developed between the dorsal and ventral valves and those in which it is absent, the latter being the more primitive.

In the Inarticulata there are five pairs and an odd muscle concerned with moving the valves. The unpaired muscle is posterior in position and serves to open the valves (diductor). The three lateral pairs (4, 5, 6) are called "protractors" and

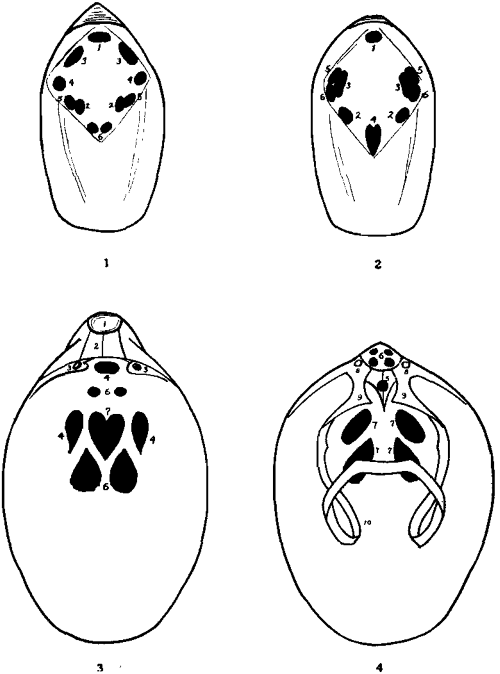

FIG. 52.—Muscle scars and other features of the interior of brachiopod shells. Inside view of ventral (1) and dorsal (2) valves of *Lingula*. 1. Scars of the diductor muscle which opens the valves. 2. Scars of the adductor muscles which close the valves. 3. Scars of the transmedial muscles which move the valves sidewise. 4, 5, 6. Scars of protractor and retractor muscles which move the valves forward and backward. Inside view of ventral (1) and dorsal (2) valves of *Terebratula*. 1. Pedicle opening. 2. Deltidial plates. 3. Sockets and 8 teeth. 4. Scar of ventral adjustor muscle which runs to the pedicle. 5. Scar of dorsal adjustor muscle which runs to the pedicle. 6. Scars of diductor muscles for opening the valves. 7. Scars of adductor muscles for closing the valves. 9. The crura. 10. The looped brachidium.

"retractors" and serve to slide the valves forward and backward on one another. A pair of central muscles (adductors) serves to close the valves. Finally, there is a pair of muscles at the sides, crossing obliquely from the right side of the lower to the left side of the upper valve and from the left side of the lower to the right side of the upper valve and called "sliding" or "transmedial" muscles, which enable the valves to move sideways on one another.

In the Articulata there are five or six pairs of muscles. The adductors or occlusors which close the valves fork midway in their course, thus leaving four scars on the inside of the dorsal valve and two scars on the ventral valve near its center. Two other pairs, called "diductors" or "divaricators," run from the floor of the ventral to the apex of the dorsal valve, serving to open them. Two pairs of muscles known as "dorsal and ventral adjustors" run, respectively, from the dorsal and ventral valves to the pedicle. These move the shell as a whole on the pedicle.

The form and ornamentation of the shells are endlessly varied. The earliest known forms of the Cambrian, like the very young of existing forms, have small, thin, unornamented shells the two valves of which are much alike.

No excessively large forms are known throughout brachiopod history, an inch or two in length or width being the average maximum, although certain species of Productus of the late Paleozoic may occasionally reach dimensions three or four times greater.

Since only the shells are found fossil, the hard parts have been minutely studied. They show many interesting features of their past evolution as well as adaptations to various habits of life. As already mentioned, the earliest forms are small, with thin, smooth, almost circular shells, the dorsal valve being only slightly shorter than the ventral and leaving a wide posterior opening between the two behind, through which the short, thick pedicle protrudes. When the free-swimming larva of a modern form commences the secretion of the shell and attaches itself, it is called a "protegulum." This is shown in the dorsal and side view in the accompanying figure and at this stage it is scarcely distinguishable from the most primitive fossil genus—Rustella of the lower Cambrian (Fig. 53[1,2]).

The principal evolutionary trends have been an increase in size; the thickening of the shell; the reduction in the relative

size of the pedicle; the development of ornamentation in the shells, usually in the form of radial ribs or folds, thus increasing its mechanical strength; the development of various internal hard parts for the more efficient attachment of various muscles; the formation of an articulation or hinge as a fulcrum for the opening and closing of the valves; the formation of calcareous supports for the arms; and modifications concerned with the exit of the pedicle.

The features connected with exit of the pedicle are those largely used for dividing the phylum into the four orders recognized, and these will, therefore, be considered first.

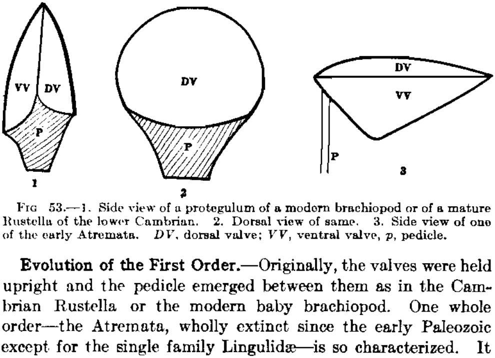

FIG. 53.—1. Side view of a protegulum of a modern brachiopod or of a mature Rustella of the lower Cambrian. 2. Dorsal view of same. 3. Side view of one of the early Atremata. *DV*, dorsal valve; *VV*, ventral valve, *p*, pedicle.

Evolution of the First Order.—Originally, the valves were held upright and the pedicle emerged between them as in the Cambrian Rustella or the modern baby brachiopod. One whole order—the Atremata, wholly extinct since the early Paleozoic except for the single family Lingulidæ—is so characterized. It represents the ancient stock from which the other three orders were derived.

Evolution in the Direction of the Second Order.—The Neotremata adaptations comprised a relative increase in size of the ventral valve, which frequently became more or less conical. With this greater growth, the hind end of the ventral valve partially or wholly enclosed the base of the pedicle either as an open triangular cleft or slit or as a closed, sheathlike hole. The diagram of Acrotreta shows the typical form and habit of the animal in this order (Fig. 53³). Many of the forms, however, in their youth discarded the pedicle altogether and cemented one of the valves directly to some foreign object (*e.g.*, Crania)

and these forms survive to the present, whereas all the pedicle-bearing Neotremata became extinct before the close of the Paleozoic.

The course of evolution of the two remaining orders took the direction of perfecting a hinge mechanism by which the two valves were articulated. In the less specialized of these orders—*the Protremata*—the shells were distinctly larger and thicker and more calcareous than in the Inarticulata. The pedicle opening was entirely restricted to the ventral valve, and the triangle-like opening was more or less restricted in front of the pedicle by the secretion by the pedicle of a plate known as a "deltidium." In the Telotremata, a pair of plates, secreted by an extension of the ventral mantle, serves the same purpose as the deltidium of the Protremata and is called "deltidial plates."

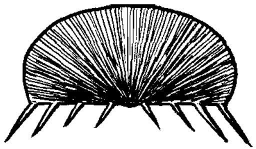

Fig. 54.—A valve of Chonetes showing the anchoring spines along the hinge.

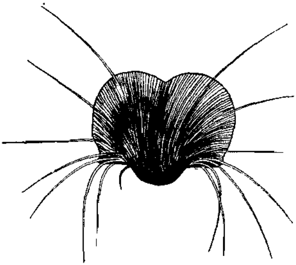

Fig. 55.—A valve of Productus showing the anchoring spines.

The Protremata is a large and progressive order, and the shells were almost invariably plicate or striate or spined. The three superfamilies into which it is divided all made their appearance before the close of the Cambrian, two of them becoming extinct near the close of the Paleozoic. The third, the Strophomenacea, show some highly interesting adaptations. The pedicle tends

to be small and is replaced by other methods of anchoring the animal. This modification may take the form of spines along the back of the short, wide valves, as in Chonetes (Fig. 54), or these spines may develop to excessive lengths on several regions of the shell, particularly on the ventral valve, as in the very prolific genus Productus of the late Paleozoic among which occur the largest known brachiopods (Fig. 55). Or the valve may be cemented directly to some foreign object, as in Thecidia, the only type of Protremata which has survived to the present. A peculiar modification of this cemented type, constituting the most extreme sessile adaptation of the whole phylum, is the genus Richthofenia of the Permian in which the ventral valve continues to grow upward around the margin until it becomes a high cone, constantly raising the animal above the mud of the bottom, the dorsal valve becoming a lid and the old part of the cone becoming filled with vesicular deposits (Fig. 56).

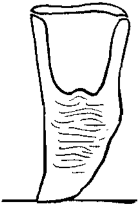

FIG. 56.—Section of Richthofenia showing the lid, living cavity, and the base filled with *vesicular deposits*.

The fourth order, the Telotremata, contains the dominant existing brachiopods. The pedicle remains functional and passes through an opening in the ventral valve, an opening which is restricted by deltidial plates. The main feature distinguishing this order from the other three is the secretion of internal calcareous supports for the arms—only incipiently developed in the superfamily Rhynchonellacea, taking the form of loops in the superfamily Terebratulacea, and the form of spirals in the superfamily Spiriferacea which became extinct in the middle Mesozoic.

The relationship, relative abundance, and geological range of all the brachiopod superfamilies are shown in the diagram (Fig. 57).

The various internal hard parts, which have been made unnecessarily difficult to understand by the cumbersome terminology invented for their description, will now be considered.

The opening through which the pedicle passes out is technically known as the "delthyrium." This opening is restricted in size to fit the pedicle by the formation of calcareous plates called, if single, as in the Protremata, a "deltidium," if paired, as typically developed in the Telotremata, "deltidial plates."

In the Articulata (Protremata and Telotremata) a hinge plate is formed on which there is a tooth on each side in the ventral valve and corresponding sockets in the dorsal valve. Any erect or oblique plates which support the hinge plate from underneath, *i.e.*, from the floor of the valve, are known as septa.

In certain forms, especially in the Pentameracea, these dental plates of the ventral valve converge downward and in addition to increasing the strength of the hinge constitute a platform for the attachment of the adductor and pedicle muscles and are then

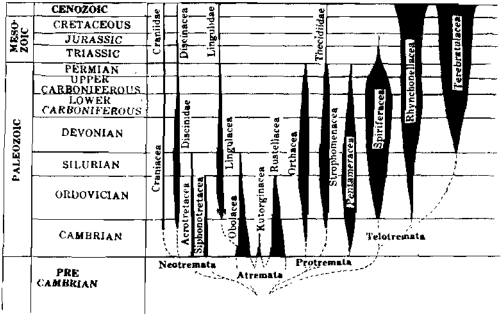

FIG. 57.—Diagram showing the relationships, relative abundance, and geological range of the superfamilies of Brachiopoda.

called a "spondylium." A somewhat similar muscle platform found in certain Atremata and more rarely in the Neotremata is called the "platform." A structure in the dorsal valve similar to the spondylium in the ventral valve of the Protremata is called a "cruralium."

These features, which are important in the proper discrimination of fossil forms, are subordinate in value and interest to the calcareous supports for the arms which develop in the Telotremata. Immediately in front of the dental sockets on the hinge plate of the dorsal valve, a pair of flat, earlike, calcareous outgrowths are formed. These are known as the "crura" and in the superfamily Rhynchonellacea calcareous secretion ceases with the formation of crura.

In the Terebratulacea, however, two ribbons of calcite grow forward into the brachial cavity, looping downward and then backward, their ends united by a transverse band. This constitutes a narrow, calcareous shelf on which the brachia or arms rest and it is consequently called a "brachidium." A brachidium may, therefore, be defined as the calcareous supports developed in the dorsal valve for the soft arms. Consequently, many of the older students call the dorsal valve the "brachial valve." The extent, form, and development of the brachidium is of great importance in differentiating genera and species.

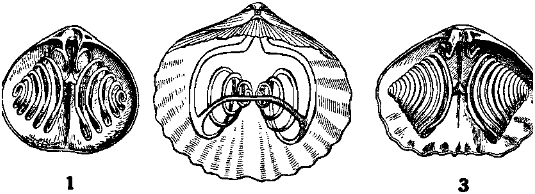
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FIG. 58.—Inside view of dorsal valves showing the spiralia of (1) Nucleospira from the Silurian (*after Davidson*), (2) Zygospira of the Ordovician (*after Hall*), and (3) Ptychospira of the Devonian (*after Davidson*).

In the extinct superfamily Spiriferacea, which ranges from the Ordovician to the Jurassic, and which is a prolific and highly important group, especially in the middle and upper Paleozoic, containing many good horizon indicators, the brachidium instead of being looped as in the Terebratulacea is spirally coiled and its right and left spirals are often called "spiralia" (Fig. 58). If the basal extensions from the crura are close together, the spirals coil outward toward the sides of the valve. If the basal extensions from the crura are divergent, the spirals may coil toward one another. The right and left spirals are usually connected by a strengthening cross-bar known as a "jugum," and the size, shape, and position of the jugum is an important diagnostic feature.

By working with a large series of shells of various ages, it is often possible to make out the successive stages in the life history of the brachidium, which throws an important light on the genealogy of its possessor. Seldom are fossils found in which the

brachidia are freely exposed and they usually have to be worked out by etching the shell with acid or alkali or by grinding it away. In many groups it is impossible to identify a species by the external form and the ornamentation of the shell, and recourse must be had to the internal features.

The existing brachiopods number about 225 species in about 60 genera. They occur in practically all latitudes and at all depths but are most abundant in warmer seas at shallow depths. All but a very few are confined to the continental slopes. Except for about 60 species which by reason of their habits have survived from the distant past, the existing forms are Articulata and of these some 25 or more represent the superfamily Rhynchonellacea and about 150 represent the Terebratulacea. Large, heavy-shelled fossil forms will indicate shallow water and hard bottoms. Since the majority are attached by a pedicle, they will not find a favorable environment in turbid waters and, hence, will be most abundant in limestones or sandstones. In muddy deposits they will be very infrequent and will be represented by Lingulæ which live in burrows in soft bottoms. Among living genera, two—Crania and Lingula—have existed practically unchanged since Ordovician times, seemingly defying evolutionary change. The great stimuli of evolution are changing environments and the modifications and adaptations thus made necessary in races to enable them to survive these changes. If an organism can find an unchanging environment and is reasonably hardy, its scarcely modified descendants may endure for ages.

Both Crania and Lingula were derived from normally stalked ancestors, but early in the Paleozoic they became modified. Crania dispensed with its pedicle and became cemented to some foreign objeet and has continued that habit down to the present. The ancestral Lingulæ retained their pedicle, but instead of using it as an anchor it became modified into a burrowing tool, and from the Ordovician to the present Lingulæ have dwelt in burrows in very shallow waters, and today their ability to withstand adversity is so great that they will flourish in polluted waters sometimes too foul for other marine organisms. Their burrows are mostly vertical, from 2 to 10 inches long. The pedicle is enlarged at the distal end and is highly contractile and regenerative. In the diagram (Fig. 59) Lingula is shown in two characteristic positions. On the right it is extended from its burrow and has its valves open and slightly twisted. Note the fringe

of bristles along the borders of the mantle. The one on the left is only partially projecting from its burrow. The valves are slightly opened and the mantle with its bordering bristles is

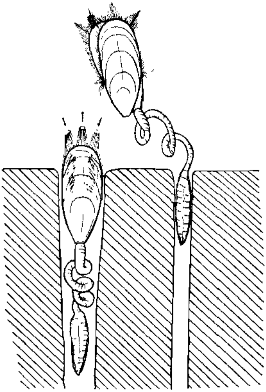


FIG. 59.—A living Lingula at the mouth of its burrow (left) and extended (right).

pursed to form three tubelike affairs, currents of water entering the side ones and passing over the arms, which are faintly visible through the shell, and passing out through the middle one, as indicated by the tiny arrows.

CHAPTER IX

MOLLUSCA

The term Mollusca, which means "soft bodied," is derived from Aristotle's name for the cuttle of the Ægean and is somewhat of a misnomer for a group which, while soft bodied, generally secretes a hard shell of one to several pieces by which members of the group are more familiarly known, as witness the name "shell-fish" commonly applied to them. They constitute one of the great groups of invertebrate animals, appearing early in the geological record (Cambrian), abundant throughout the whole of that record, and with all the great groups (classes) common at the present time, no group of higher rank than an order having become extinct.

The Mollusca include such familiar forms as oysters, clams, snails, slugs, and squids, and despite their diversities of appearance and habits of life, they all conform to a readily recognizable ground plan of organization and possess a large number of common structural features not present in any other group of organisms, which also render their recognition easy.

This ground plan is that of an unsegmented bilaterally symmetrical body with a mouth at one end and an anus at the other. Thus, there is a right and left and an upper (hæmal) and lower (neural) side. The ventral side usually gives rise to a muscular organ known as the "foot," variously modified in the different classes for creeping, burrowing, or swimming. The integument of the dorsal face is produced at its edges into a free fold like a skirt and known as the "mantle" (pallium) and between the mantle and the enclosed part of the body is a cavity or chamber (pallial or mantle cavity) from the walls of which protrusions differing in the different groups form the gills (ctenidia or branchia). The epidermis of the dorsal part of the body and mantle usually secretes a calcareous covering of one or more pieces known as the "shell."

These shells exhibit an almost endless variety of shape, ornamentation, and coloration, and since every elementary student

in biology dissects a squid, snail, or clam, and since the fossil forms are usually known from the shells alone, the chief emphasis in the present account will be on the shells.

The free body surface is covered with an epithelium, frequently ciliated, and richly supplied with nerves and glandular cells, the latter secreting an abundant mucus which is such an unpleasant feature of the live animal. The alimentary, circulatory, nervous, and generative systems are well developed and may be very briefly described.

The alimentary system is relatively simple, with two openings, originally at opposite ends of the body but frequently (except in classes Amphineura and Lamellibranchiata) brought closer together by a ventral bending, which in the Gastropoda is accompanied by a rotation. The alimentary canal comprises three parts—a front part (œsophagus and buccal cavity), a median dilation or stomach, and a hinder part or intestine. Its walls, especially toward the front end, may be provided with horny growths, as the prehensile collar around the mouth in Doris, the beaklike mandible of Nautilus, the platelike chewing or grinding pieces present in occasional other forms, and, more especially, the so-called "tongue" or "radula" which is an outstanding feature of the phylum (lost in the Lamellibranchiata).

The radula is secreted in a pouch immediately below and behind the mouth and consists of a cartilaginous ribbon covered with rows of tiny, chitinous teeth. It is operated by appropriate muscles and can be protruded from the mouth and worked like a file. It may be longer than the body, being coiled at its hind end; and the number of teeth in a row, the number of rows, and the character of the teeth, *i.e.*, whether all are alike or the central ones larger, are much used in classifying existing forms. Since the radula is never preserved in the extinct forms, paleontologists cannot utilize it. In Amphineura, Gastropoda, and Cephalopoda one or several so-called "salivary glands" empty into the buccal cavity. A very large and important gland, the so-called "liver" (physiologically a pancreas), discharges into the stomach.

In addition to the alimentary system there are two other cavities within the molluscan body. The one generally called the "cœlomic" or "body cavity" comprises the pericardial, renal, and genital and communicates with the exterior. The second, a remnant of the segmentation cavity of the embryo (blastocoel), is continuous with the spaces in the ground tissue

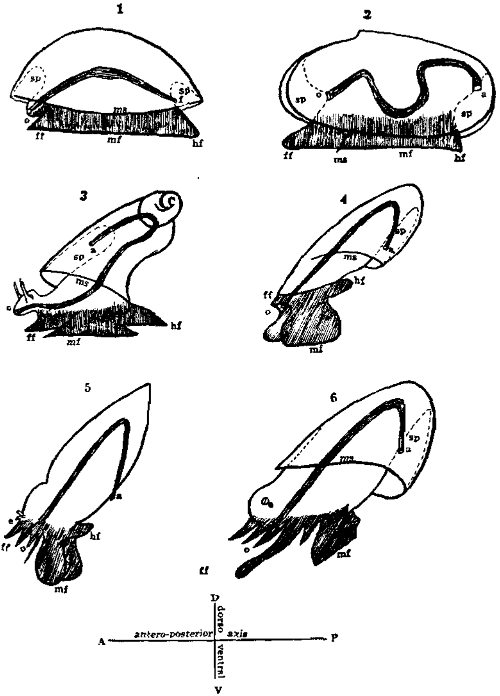


FIG. 60.—Diagrams of different Mollusca to show their morphological orientation and principal parts. (*After Lankester.*) 1. Chiton. 2. Lamellibranch. 3. Gastropod. 4. Thecosomatous pteropod. 5. Gymnostomatous pteropod. 6. Cephalopod. *o*, mouth; *a*, anus; *ms*, mantle edge; *sp*, pallial chamber; *ff*, fore foot; *mf*, midfoot; *hf*, hind foot; *e*, eye.

(connective tissue) of the body and constitutes the circulatory system. It is filled with a fluid blood and is both nutritive and respiratory in function. The pulsatile portion or heart is usually well developed, generally situated on the dorsal side of the pericardium and originally toward the hind end.

Blood may be colorless, blue, or red. Coloring matter may be in solution (Planorbis) or organized into corpuscles (Arca). Blood is voluminous and may be used to keep the body inflated (turgescence) when the muscles are relaxed or for protrusion of soft parts such as the foot beyond the shell.

Respiration.—In all except small forms which obtain oxygen through the general body surface, gills are developed which project into the water within the mantle cavity. There may be one or many pairs of gills, originally situated in the hinder part of the mantle cavity. Their number and structure are largely utilized in classification.

Sensation.—The function of general sensibility is developed throughout the exposed body surface and localized at the more exposed parts such as the tentacles of the gastropods, the ends of the siphons, and the edges of the mantle in the bivalves. Primitively organized organs of taste, smell, and hearing are present in many forms and, except in the Amphineura, Scaphopoda, and Lamellibranchiata, well-developed eyes, of extraordinarily large size in the Cephalopoda, are present.

The nervous system comprises a collar around the œsophagus from which two cords extend backward and are more or less connected by cross-branches and ganglionic enlargements.

Sexes.—In general, the sexes are distinct and frequently differ in size and other features. The generative organs are primitively paired and develop in the walls of the body cavity. Some forms copulate; in others, the eggs are discharged before fertilization. They are discharged separately in Amphineura, Scaphopoda, Lamellibranchiata, and the more primitive Gastropoda, *i.e.*, in the non-copulating forms. In the majority of the aquatic Gastropoda and in the Cephalopoda they are laid in a gelatinous matrix which frequently hardens into egg cases of extraordinary shapes and sizes. Some forms retain the eggs until they hatch in the mantle cavity or a special pouch, but the vast majority do not. The number of eggs is roughly proportionate to the subsequent care taken of them. In forms which leave them to chance, such as the oyster, they number several millions and

hatch quickly into free-swimming larvæ. Where they are incubated they are much fewer in number *e.g.*, 20 to 100 in the pond snail (Limnæa), and are more like their parents when hatched. *The eggs are more numerous in marine than in fresh-water or terrestrial forms* and, in general, can survive cold more readily than heat.

Development.—The fertilized egg cell undergoes unequal segmentation and in the majority of Mollusca is hatched as a small, pear-shaped, ciliated larva known as a "trochosphere" and this by growth and modification become a veliger and grows gradually to the adult form.

Bionomics.—The Mollusca originated in the shallow seas, and the vast majority have remained aquatic and marine. No Amphineura, Scaphopoda, or Cephalopoda have become adapted to fresh water and but few Lamellibranchiata (Cyrenidæ, Unionidæ, etc.). The terrestrial forms are all Gastropoda and represent but few groups, although varied and individually numerous.

Mollusca are found in all latitudes, at all depths in marine and fresh waters, and at all altitudes on the land but are most abundant in the shallow waters around the continental margins. As a rule, they are free and crawl, swim, or burrow. A very few, chiefly Lamellibranchiata, are sessile throughout their adult life. Some few live in association (commensals) with other invertebrates and a still fewer number have become adapted as external or internal parasites, chiefly on or in the Echinoderma.

Many mature in a single season, others require a longer period, and their life span varies from a few years (Pulmonates) to a score or more (Littorina). Adults are much hardier than their eggs or larvæ, differing through wide limits in their ability to withstand changes of salinity, temperature, etc. They vary in size from almost microscopic to the 500-pound surf clam (Tridacna) of the Pacific or the giant squid (Architeuthis) of the North Atlantic which with its extended tentacles is over 50 feet in length. Some are formidable carnivores, others feed on organic mud or microscopic organisms. The habits and form are endlessly varied and no group furnishes more interesting adaptations or illustrations of evolution. Fully 50,000 species are known. About half the living forms are Gastropods.

Fresh-water and deep-water forms have thinner and smoother shells. Pelagic and abyssal forms are generally colorless or bluish. Burrowers and parasites are simplified and tend to lose

those parts—eyes, for instance—for which they no longer have use.

CLASSIFICATION

Because of the large number of collectors of shells and the fact that there will always be known many times as many shells as shell inhabitants, even among existing forms, the shell was long the chief criterion in classification. It is, of course, an index of relationship much less reliable than the structure of the soft parts.

The Mollusca are usually divided into the following five classes:

Shells of two pieces, a right and left	Lamellibranchiata
Shell of one piece:	
An arcuate tube	Scaphopoda
A long or short cone, generally coiled in an ascending spiral	Gastropoda
Generally absent or coiled in a planospiral	Cephalopoda
Shell of several pieces	Amphineura

Most of the more familiar forms and the vast bulk of the fossil species belong to the classes Lamellibranchiata, Gastropoda, and Cephalopoda. Since the Amphineura are, in some respects, more like the original stock from which the phylum took its origin, it will be convenient to start with them.

CLASS AMPHINEURA

This class of mollusks, known as Chitons, includes two groups. One, the Aplacophora, comprises wormlike forms in which the shell has entirely disappeared. The skin is studded with calcareous spicules and none of the dozen existing genera is found fossil. The second group, the Polyplacophora, have a shell of eight curved plates in a central dorsal row articulating with one another. These are held together by a flexible spicular band, the girdle. The head is not much differentiated but possesses a radula. The alimentary canal is nearly straight. A large-soled foot occupies nearly the whole of the ventral surface, and a row of gills projects into the shallow mantle cavity on each side of the foot between it and the edge of the mantle (Fig. 60[1]). Each shell piece is two layered and in the higher forms the inner layer projects beyond the outer, forming what are known as "insertion plates" which are embedded in the mantle at the sides

and extend under the plate immediately in front so that the animal can roll up like an armadillo or pill bug. There are several hundred existing species widely distributed. Less than 100 fossil species are known. These are often based upon detached plates and are of slight paleontologic importance. They are divided into three orders based upon the featnres of the insertion plates. In the Eoplacophora, which includes a Paleozoic family and a Tertiary to Recent family, insertion plates are either not developed or, if present, they are entire. In the Teleoplacophora, which includes the Tertiary and Recent family Chitonidæ, the insertion plates are cut by slits into grooved teeth. In the Mesoplacophora the insertion plates are similarly slit into teeth but the teeth are not grooved. This order includes four Recent families, three of which have been found fossil in the Tertiary.

CLASS GASTROPODA

Definition.—Gastropoda are mollusks in which the three external divisions of the body—the head, mantle, and foot—are well defined. The head is well developed and carries specialized sense organs. The foot lies wholly behind the head and is conspicuously soled and used for creeping, except in a relatively

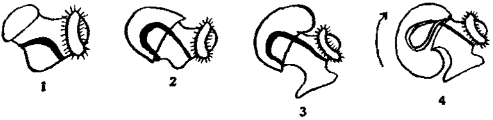


FIG. 61.—Diagram showing the stages in a larval gastropod illustrating how gravity may have developed the twisting of the soft parts.

few forms which have become adapted for a pelagic swimming life in which the foot is modified into a fin (Heteropoda) or a pair of fins (Pteropoda). The mantle is undivided and usually secretes a single shell, primitively saucer or cup shaped, usually a high cone coiled in an ascending spiral. The outstanding difference between gastropods and all other mollusks is the lack of symmetry of the principal organs. This can be most readily understood by the rotation of the developing shell and visceral hump during the early stages. The free-swimming larva (veliger) is like that of its relatives with the gills and anus toward

the hind end of the body. As it grows upward and forward, its center of gravity becomes adjusted by rotation which forms a loop in the alimentary canal and brings the anus to the front and over the body. The right gill assumes a position to the left of the center and the left gill atrophies. The nerve trunks are also looped by this rotation. This rotation is shown Fig. 61.

A siphon may carry fresh water to the gill from the front end of the aperture and a second siphon at the hind end of the aperture carries off the waste products. A radula, often of great length, is normally present.

The Shell.—The shell is secreted by the mantle and the epidermis of the visceral cone. It consists of an organic base infiltered, usually with calcium carbonate of the mineral form known as "aragonite," and normally consists of three layers made up of microscopic oblique prisms laid in different directions in each layer.

The shell is a cone which is wide and low in the more primitive genera of the early Paleozoic and in the modern limpet-like forms; but a narrow and high cone in the more familiar types, and *coiled, usually in an ascending spiral. If the inner part of the* coils are in contact they form an axial pillar known as a "columella." If the coils on their inner part are not in contact but coiled around an imaginary axis, there is a central canal-like space along the axis and this is known as an "umbilicus." The more frequently used terms in describing a shell are shown in the accompanying diagram. Each coil is called a "whorl," the latest formed and largest being known as the "body whorl," and all of the earlier whorls constituting what is called the "spire," where they meet on the outside is the "suture." The shell opening is the "aperture" and its border the "peristome." Where notches or channels interrupt the border in front for the brachial or behind for the anal siphon the peristome is divided into an outer and inner lip, which may have an overlay of calcareous material, especially on the inner lip (callus), and may develop folds. The outer lip may be variously thickened or ornamented. The outer surface of the shell may be smooth or ornamented in a great variety of ways, *i.e.,* raised lines (liræ), ribs (costæ), depressed lines (striæ), grooves (sulcæ), furrows, spines, and nodes, or various combinations of these. All of *these are arranged across the axis of the cavity from suture to* suture and thus parallel with the axis of the shell and are then

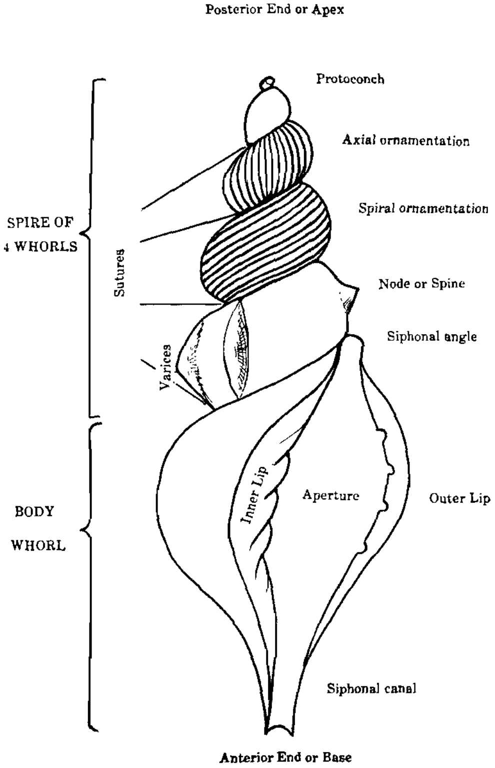


FIG. 62.—Diagram showing the principal parts of gastropod shells.

axial, or they may be arranged parallel with the cavity and parallel with the suture, in which case they are spiral and are oblique to the axis of the shell. A node is a low, rounded or conical elevation not sufficiently narrow and extended to be called a "spine." Sometimes a node will extend all the way across a whorl from suture to suture in which case it is called a "varix" (plural, varices). All these external ornaments are formed by the mantle edges around the aperture during the earlier life history. The little free-swimming larva forms the initial shell (protoconch) which is frequently to be seen on the tip of the spire. Since the shell thus preserves the size and form of each season's growth throughout life, differences in shape or ornamentation at different stages may frequently be observed.

Some shells are low cones and the earliest known were cup or helmet shaped. Some few are coiled in one plane (planospiral like Bellerophon or Planorbis). Usually, the spiral is an ascending one, the *coiling being from left to right* like the hands of a clock turn. This is right-handed or dextral coiling. A relatively few are coiled from right to left or counterclockwise. These are left handed or sinistral. In the diagram the normal coiling is shown with the aperture on the lower right. If a left-handed (sinistral) shell were shown, the aperture would be on the lower left instead of the right. When the soft animal grows so rapidly that it covers the early whorls, the last or body whorl may completely conceal the earlier whorls as in a cowry (Cypræa). Such a shell is said to be convolute.

A few gastropods have an irregular shell (Vermetus). The relative proportions of the body whorl and spire and the number of whorls give us the endless shapes we see, from the slender, high-spired Turritella to the globular, low-spired Natica. The animal is attached to the shell by a muscle known as the "columellar muscle," the contraction of which pulls the animal in, the last part being the upper surface of the hinder part of the foot which may develop a horny plate, rarely calcified, which fits the aperture and forms a lid or door known as the "operculum."

Habits.—Gastropods are prevailingly aquatic, and the greatest variety as well as all of the more primitive living types occur in shallow marine waters, although a few are found at all depths. A relatively few inhabit fresh waters and the land snails (Pulmonates) are enabled to maintain a terrestrial existence by

modifying the mantle cavity into a sort of lung, sealing the shell aperture, and hibernating during periods of dryness. Most marine forms cannot live in fresh water but a few (Cerithium, *Littorina, Trochus, etc.) are not affected. Similarly, most* fresh-water forms die in salt water but a few, like Melania, Limnæa, etc., are hardy.

The majority crawl by an undulatory motion of the sole of the foot, some burrow in the bottom (Natica), a number, like the limpets, are sedentary and cling closely to rocks by their foot or become firmly attached by the secretions of a calcareous plate by the foot (Hipponyx). The Strombidæ jump by suddenly contracting the foot.

A considerable number of small forms have become adapted to a pelagic life and swim by flapping their two-winged foot These are the sea butterflies (Pteropoda) which are sometimes considered a separate class. Although the majority of gastropods are herbivorous, many subsist on decomposing animal matter, and some, like the drills, are predaceous and prey on other mollusks. A few have become parasitic.

Fossil forms occur from the Cambrian to the present. The first great increase in modern forms is during the Cretaceous and most of the early Tertiary genera still exist. The oldest known land snails are found in the Carboniferous.

CLASSIFICATION

The basis of gastropod classification is the character of the gills and foot, the structure of the reproductive organs and nervous system, and the position of the heart—all features of the soft body, not determinable in fossils. The character of the shell and the structure of the radula are distinctive for the smaller groups. Since very few of the families of gastropods have become extinct, however, it is not difficult to refer the fossil shells to their proper place in the classification, even though this is based so largely on the soft anatomy. Among the Cambrian gastropods are found a number of conical shells (Scenella, Archinacella, Palæacmæa) like those assigned to their hypothetical ancestry. Also, large pteropods are found and planospiral shells like Bellerophon as well as shells coiled in an ascending spiral. It is thus evident that the ancestry of the class goes back to pre-Cambrian times. The earlier forms tend to have round, entire apertures and the shells tend to be smooth or but

slightly ornamented. During the Paleozoic, the two-gilled Aspidobranchia predominate and the families Raphistomidæ and Hyolithidæ become extinct. During the Mesozoic, aspidobranchs are overshadowed by the forms in which the left gill becomes suppressed. Thirty families of Ctenobranchia and nine families of Opisthobranchia make their appearance in the geological record, and a few families become extinct (Euomphalidæ, Trochonematidæ, Purpurinidæ, Nerineidæ, Columbellariidæ). Thirteen families are added in the Tertiary, and some few Recent families have no discovered fossil forms. Of all the classes of mollusks the Gastropoda may be said to be at their zenith of variety and abundance at the present time.

CLASS SCAPHOPODA

Definition.—Small, marine, bilaterally symmetrical, elongated, and cylindrical; the mantle margins united into a tube open at both ends and lining the curved tubular shell. The head has become rudimentary and has lost its eyes, but the mouth has retained a radula. Foot long conical and lobate, adapted for burrowing. Gills wanting and respiration performed by the inner surface of the mantle. Heart a single-chambered dilation of circulatory system, sexes separate. Shell a narrow, elongated, slightly curved cone, the larger end anterior and the smaller posterior; the concave side dorsal and the convex side ventral. Approximately round in cross-section, smooth or longitudinally ridged. In some forms the hinder end of the shell has a ventral notch or slit.

Habits.—The animal lives in the bottom, from shallow water to depths of 15,000 feet, buried obliquely, with the small end projecting into the water. There are about 200 living and 300 fossil species all much alike and unimportant. Doubtfully represented in the older Paleozoic by Lævidentalium and several of the existing genera going back to the Cretaceous. The only common fossil forms are referred to the genus Dentalium in which the shell is larger and tapers uniformly from front to back, and Cadulus in which the shell is uniformly small and tapers toward both ends.

CLASS LAMELLIBRANCHIATA

The Lamellibranchiata, or Pelecypoda (hatchet footed), as they are commonly called in this country, are one of the most interest-

ing groups of mollusks from the point of view of adaptation. Some authors would call the simplification of the lamellibranchs by which they have become almost perfectly adapted for their mode of life "degeneration," but the effective adjustment of an organism with its environment is just as much a specialization when it is attained by reduction and simplification as when it is reached by increased complexity of structure.

The vast majority of the lamellibranchs are bilaterally symmetrical animals both as regards their soft parts and as regards their containing shell, which is of two pieces, or "valves" as they are called. They are all bivalved and aquatic, and the vast majority are marine. The internal anatomy is relatively uniform throughout and can be correlated with shell form much more definitely than is the case in the Gastropoda. The head is vestigial, that is, it has been almost completely suppressed during their evolution. The mouth has lost any traces of jaws and of the radula that is present in all other classes of mollusks, for the reason that the lamellibranchs feed on material water borne on a current set up by the action of cilia and, hence, minute in size. The mouth is at the front end and the anus at the opposite end of the animal. The viscera are enclosed in a right- and left-lobed mantle which secretes the right and left valves of the shell, hanging down like a curtain on each side. Within these mantle flaps are the right and left gill cavities into which the gills project and from the central median lower side of the body is suspended a muscular extensile organ—the foot. It lacks a sole in all except the most primitive known forms and is usually compressed and remotely resembles a hatchet shape when viewed from the side, which suggested the name Pelecypoda for the class. The foot is adapted for burrowing in the majority of the lamellibranchs. The lower edges of the mantle are separate in more primitive forms but become partially united in the more specialized forms, as will be explained later.

The Shell.—The shell consists of a right and left valve which are the counterparts of one another and no shelless form is known. The free-swimming larva (see Fig. 1^5) is provided with a single, dorsal, saddle-shaped shell gland which early begins secreting a tiny transverse cylinder or pellicle which starts to become calcified at the two ends. Each of these ends becomes a valve and the median uncalcified portion becomes the ligament. Each valve is essentially a low, wide cone which increases in size at

its margin by seasonal concentric increments which are secreted by the edge of the mantle. Since this growth is limited above and is most rapid downward and generally backward, the cones

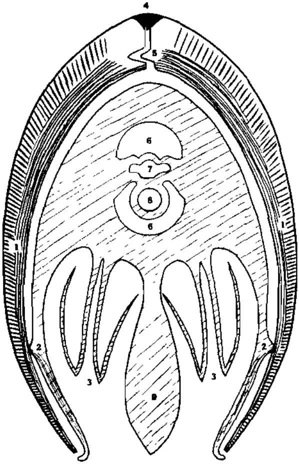


FIG. 63.—Median cross-section of a lamellibranch showing the right and left valves (1) *with inner lamellar, middle prismatic, and outer horny layers.* Dorsally is the elastic ligament (4) which pulls the valves open when the adductor muscles are relaxed. The hinge (5). Lying snugly but freely within the valves is the soft body of the animal and sections of the pericardial cavity (6), the heart (7), and intestine (8), are seen. From the ventral side the central foot *hangs down (9), also the gills (3), which are in the longitudinal chambers between* the foot and the mantle. Note the attachment of the mantle to the shell at (2) which leaves the narrow scar known as the "pallial line," and from which tiny muscles extend downward into the mantle flaps to pull it in when the shell is closed. Note, also, the recurved mantle margin which secretes the prismatic *and horny shell substance, the lamellar part being secreted by the whole outer* surface of the mantle lying against the valves.

become oblique. The apex of the cone is the beak or umbo, and the base of the cone is the entire margin of the valve. The shell consists typically of three layers—an outer horny layer (periostracum) not easily corroded and protective in function, which is lost during fossilization; inside the periostracum is a

prismatic layer secreted by the edges of the mantle and composed of tiny prisms, generally of calcite; the third or inner layer is made up of thin plates or lamellæ, often of aragonite, which is secreted by the whole surface of the mantle in seasonal layers and which, hence, is thicker in the older part of the shell inside the beak than it is toward the margins. The valves are united by a dorsal ligament and internally by one or two transverse muscles known as "adductors." The muscles close the shell and the ligament opens it. The valves are generally equal except in very sedentary or sessile forms in which the attached valve becomes larger and the free valve becomes more or less of a lid. They usually lie on their right side (Pinna, Spondylus, Plicatula, Anomia, Rudistids) but may lie on their left (Ostrea, Exogyra, Chama). The principal parts are shown in the diagram (Fig. 63).

Ornamentation.—The exterior of the valves shows the regular concentric seasonal growth lines, which may be supplemented by a variety of additional concentric processes and by radial markings, ranging in size from lines to ribs or folds, often produced as plates or spines where the radial and concentric intersect. The growth lines are formed by the mantle edges and the other features by temporary or permanent extensions of the mantle edges.

Above the hinge in the less specialized forms is an area lying between the beaks known as the "cardinal area" in which the surface has a different ornamentation from the rest of the shell. In more specialized forms this becomes modified by the shifting of the beaks forward and the axis of rotation backward, and the front part (the lunule) is separated from the back part (the escutcheon).

The more primitive sort of cardinal area is shown in Figs. 3*C* and 4*C* of Fig. 64 as it occurs in the genus Arca. In such a type, the valves are more nearly symmetrical, and the beaks *B* are far apart. In more advanced forms, where the valves extend backward much farther than they do forward, the axis of rotation has moved behind the beaks and they are close together and pointed forward. What remains of the cardinal area is represented by the lunule I in front of the beaks *B* and the escutcheon *E* behind the beaks, as shown in Figs. 64^1 and 64^2 for the genus Venus. When the beaks are directed toward one another, they are said to be straight ("orthogyre"); when they are directed

forward, as in Venus, they are known as "prosogyre"; and when they are directed backward, they are known as "opisthogyre."

The original lamellibranchs were small and thin-shelled forms, with a dorsal central external ligament, with subequal muscles *high up in the shell, and without siphons* or *pallial lines*. With the gradual increase in the size of the shells, the first mechanical difficulty to be overcome was the actual strength of the material. This increase in strength was provided in some forms by simply increasing the thickness of the valves. Other forms solved

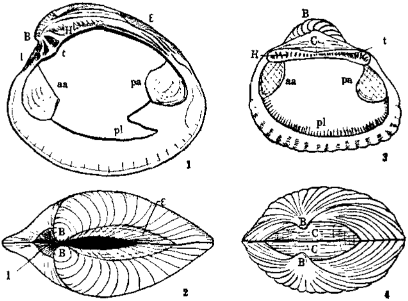


FIG. 64.—Inside view of right valves (above) and of the two valves from the dorsal side (below) of (1, 2) Venus and (3, 4) Arca, showing beaks: *B*, hinge; *H*, teeth; *t*, muscle scars; *aa* and *pa*, pallial line; *pl*, lunule; *l*, escutcheon, *E*, and complete cardinal area, *c*. The ligament is shown in Venus in solid black. About half natural size.

the problem more effectively by increasing the curvature of the valves on the familiar principle of the arch—the greater the curvature the greater the strength for the same amount of material. Others substituted a series of small arches on the main arch of the valves, as is illustrated by such ribbed or plicate forms as a Pecten or a Tridacna.

With the general increase in size with the evolution of the lamellibranchs, there was the well-marked tendency for this increase to be greatest downward and backward because of the increased size of the intestine due to a less concentrated diet, and the posterior mantle edges united in various ways to maintain the water and food currents as the animal buried itself more and more in the bottom. Hence, as the shell grew more rapidly

backward and downward the hinge line or axis or rotation moved backward, the posterior adductor had most of the work to do, and the anterior adductor remained high up in the shell and small in size and eventually disappeared altogether. These contrasts in the muscle scars were once used as a basis for classification—those shells in which both were present were known as the Dimyaria; if the two were equal they constituted one division of the Dimyaria known as the Isomyaria; if unequal the Heteromyaria or Anisomyaria; or if the anterior was absent at maturity they were known as the Monomyaria. As the state of development of these scars was due entirely to the shape of the shell which, in turn, was a consequence of the habits of the animal, the character of the muscle scars were due to adaptation and might occur in any group, so that their condition was no clue to relationship.

A second mechanical difficulty to be overcome during the early evolution of the bivalves was the tendency for the valves to rock when they were pulled shut and, hence, not to close accurately, thus exposing the occupant to the dangers of predatory enemies or noxious substances in the water, such, for example, as mud which would foul the gills and suffocate the animal. This difficulty of closing promptly and accurately was augmented as the shells became unsymmetrical, *i.e.*, larger behind than in front. This problem was solved by the same means as the third problem which was to lock the valves in some way so that when closed they could not slide over one another or be rotated. If the difficulty of keeping two saucers or two cups edge to edge be considered, the problem facing the primitive Lamellibranchiata can readily be understood.

These last two problems were solved in a variety of ways by developing uneven and scalloped edges along the dorsal and ventral margins. These would serve as guides in closing and would prevent slipping or rotation when closed and it is believed that the specialized hinge plate with its teeth was derived by the modification of such primitive interlocking irregularities along the dorsal edges of the valves. A pair of valves of a hard clam, a cockle, or almost any bivalve have only to be examined in order to prove how effectively and in what different ways this guiding and locking problem has been solved.

Origin of Hinge Teeth.—We may now consider the manner in which the origin of hinge teeth may be explained: As soon as

the originally smooth shells developed ribs these would form denticulations on the margin, as in a modern cockle or pecten. In the modern forms they are strongest along the ventral margin and become reduced toward both the front and hind margins. In many Paleozoic forms this ribbing is present along the dorsal margin. Remembering that the beak of the valve is the apex of the low cone which constitutes what is called a valve and that the ribbing radiates from beak to margin, there will be no diffi-

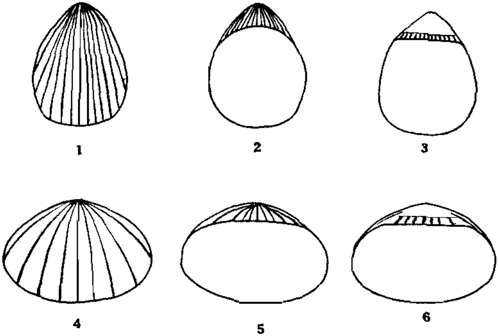


FIG. 65.—Diagram showing how the form and ornamentation of the primitive shell may have determined the character of the hinge teeth. 1, 2, and 3, leading to taxodont; and 4, 5, and 6, leading to teleodont hinges.

culty in understanding this theory. The size and spacing of these marginal teeth depend on the size of the radial arches or ribs that ornament the shell. In forms in which the ribbing was closely spaced and in which the outline of the valve was symmetrical and, perhaps, slightly higher than long, the denticulations of the apex of the dorsal margin would act as a fulcrum. They would, of course, be highly inefficient unless the arc formed by the top margin flattened, that is, became straight, since an axis of rotation must be a straight line, a tendency exemplified in all bivalves. The outside of such a valve would look something like that shown in Fig. 65^1, the inside like Fig. 65^2, and by a straightening of the dorsal margin a row of similar hinge teeth

would result like that shown in Fig. 65[3] which is like that found in Arca, or in one of the most primitive existing genera—Nucula.

If the original shell form was longer than high and if it be assumed for the sake of the illustration that it had fewer stronger ribs, as shown in an outside view in Fig. 65[4] and an inside view in Fig. 65[5], then, as the margin straightened, the central marginal teeth would do most of the work and those at the ends would tend to remain feeble and long, and the intermediate would tend to remain undeveloped or small as in Fig. 65[6]. Some such series of changes would result in a familiar type of hinge, exemplified by many modern shells which have a few strong cardinal teeth in the middle and lateral teeth parallel with the margin.

It must be realized that the actual series of changes were not so simple as the illustrations, for the shell was changing in form and symmetry at the same time, the beak was changing its direction slightly, and the axis of rotation was shifting more or less backward.

Types of Hinges.—A considerable number of hinge types are recognized by students, but most of them are not so well differentiated as to be clear to the beginner, since the teeth are largely moulded by the mechanics of their situation and they are, hence, easily modified or augmented by supplementary deposits secreted by the dorsal part of the mantle. Teeth, or even the whole hinge plate, may become obsolete through disuse, especially in large, fleshy forms in which the body outgrows the shell, the valves of which never close, or in others, like the pholads, living in burrows and not closing their valves.

Since laterals and cardinals are complementary in function, where the ones become strong the others become weak or absent. For example, the common hard clam, *Venus mercenaria*, has strong cardinals and no true laterals, their place being taken by a posterior, roughened, interlocking area—a sort of amorphous lateral. In the related Mactra the cardinals are gone and there are well-developed laterals. The ventral margins of the valve may have strong interlocking ribs as in many pectens and the hinge teeth may practically disappear, or the shell may be thrown into radial folds which both guide the valves in closing and prevent rotation when closed so that the hinge structures have not kept pace with the growth of the shell.

Of all of the proposed types of hinges there are but two that stand out clearly and are easily recognized. These are the

"taxodont," whose origin was suggested in the Figs. 65[1,2,3] in which the hinge consists of a series of mostly similar alternating teeth and sockets—35 teeth in each valve of *Nucula radiata*, 25 in *Glycimeris undatus*.

The second type, known as the "teleodont," consists of a few large, interlocking cardinals; Venus has 3 in the right valve and 2 in the left, Tivela has more; with or without laterals.

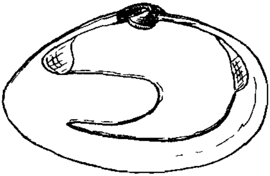
Several ingenious formulas have been proposed for recording hinge characters. Thus, that of *Venus mercenaria* may be expressed: $\frac{Lx01010}{Rx10101}$, in which L indicates the left valve and R the right and from back to front there lies x, a roughened area in each valve, and the numerals represent cardinal teeth and the zeros their corresponding sockets in the opposite valve. That of *Tellina interrupta* is written thus: $\frac{L11010l}{Rl01011}$ and shows that the left valve has a strong posterior lateral tooth 1, then a cardinal, a socket, a second cardinal and socket, and a feebly developed lateral at the front indicated by writing the *l* in italics. The right valve has 2 cardinals but it is the posterior lateral that is feeble and the anterior lateral that is strong in this valve.

The formula of a taxodont hinge may be illustrated by that of *Glycimeris undatus:* $\frac{L10(11)\ .\ 10(14)}{R01(11)\ .\ 01(14)}$ in which the center is indicated by a period and there are, hence, 11 similar teeth and sockets behind the center and 14 in front, the number in parenthesis indicating the number of repetitions of units and zeros.

There are other systems that are used by some students but, in general, it may be said that too many supposed types of hinges have been recognized and that their use in indicating relationships has frequently been exaggerated.

The Ligament.—The ligament is a fundamental feature of the lamellibranchs used for opening the valves and rudimentary in only those highly specialized forms like the pholads or rudistids in which its function is not necessary. It has always been an essential part of the hinge mechanism and has shared in the evolution of the latter. The original ligament was thin and external and worked like a C-spring or thin band of rubber, becoming stretched when the valves were held shut by the adductor muscles and contracting and pulling the valves open as soon as the adductors relaxed. With the gradual increase in thickness

of the dorsal part of the valves the ligament tended to thicken and move slightly inward. As long as it was thin only tensional or stretching elasticity was developed. As it thickened the outer part stretched but the inner part would be compressed so that both tensional and compressional elasticity were developed in two different zones and the boundary would remain neutral, and there would be a tendency for the outer and inner zones to become separated and for the one or the other to assume most of the work and remain functional and for the other to become weaker and rudimentary or disappear altogether. In a very few cases, the two remain and there are then two elastic bodies,



1

2

FIG. 66.—Interior of left valve (1) and cross-section of the two valves (2) of a *soft clam (Mya) showing character of the hinge, muscle scars, pallial line, pallial sinus*, and the manner in which the chondrophore works. Resilifer in solid black in Fig. 2.

the outer dorsal or ligament proper with tensional elasticity tending to pull the valves open, and the inner or more ventral with compressional elasticity tending to push the valves apart, the two working reciprocally.

The inner ligament is known as the "resilium" but is often improperly called the "cartilage" or "internal ligament." This resilium is usually somewhat hourglass shaped, with its expanded ends fitting into excavations on the opposite hinge plates, and such pits are known as "resilifers" (often wrongly called "cartilage pits"). If the valves become very thin as the result of a burrowing habit, as in our common soft clam (Mya), one valve may have such a resilifer and the other valve may develop a spoonlike projection from inside the beak to oppose it. Such a development is known as a "chondrophore," and it operates as shown in Fig. 66.

A chondrophore is concerned solely with forcing the valves open when the adductor muscles which hold it shut relax, and it must not be confused with the somewhat similar-looking process in some of the pholads. The latter, known as a "myophore," has nothing to do with the opening of the valves but is an internal support for the viscera.

When the normal ligament extends both in front and behind the beaks, it is said to be "amphidetic," as in Glycimeris. When it lies wholly behind the beaks, as in Venus, it is said to be "opisthodetic."

The Mantle.—All lamellibranchs must provide a water current over the gills, for respiratory purposes, and to the mouth, for feeding purposes. The earliest and most primitive forms had no siphons, and the opposite mantle edges were entirely free and

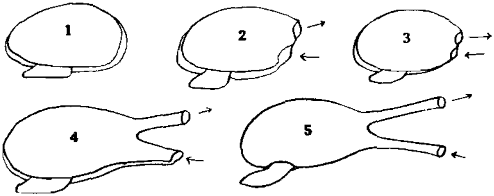


FIG. 67.—Diagrams showing the condition of the mantle margin and the formation of siphons in various lamellibranchs. 1. Open mantle. 2. Mantle margins united at one hinder point. 3. Mantle margins united at two hinder points. 4. Two siphons formed by the posterior extension of the mantle margins, but the inhalant one open along its lower edge. 5. Mantle completely closed except for an opening for the foot.

open all around. The necessity for setting up inhalant and exhalant currents and for preventing the two from mixing is obvious. If this were not done, water fouled with waste products or, perhaps, deprived of its oxygen would bathe the gills. This has been provided against by various modifications of the mantle margins. In some instances, the posterior mantle margins were folded so as to develop inhalant and exhalant conduits without any actual union of the edges, as in Unio or Trigonia. Usually, however, the mantle margins have become united with one another to a greater or lesser degree and, in extreme cases, closed all around except for a slit for the protrusion of the foot.

In the diagrams shown in Fig. 67 the shell is removed and Fig. 67^1 shows the primitive open mantle such as is found in Nucula, Anomia, Arca, Trigonia, Pecten, etc. The first and incipient stage in the formation of siphons is for the hinder part to form a fold separating an upper or exhalant channel from a lower or inhalant channel without any union of the opposite edges. A stage slightly more advanced is shown in Fig. 67^2 in which the edges of the mantle have united to form an incipient exhalant siphon but are separate below and merely held together to form an inhalant current. This type occurs in Meleagrina, most mussels, and fresh-water clams.

The next step is for the mantle edges to unite at two points, as in Fig. 67^3. The edges thus joined grow outward to form two long tubes as shown in Fig. 67^5 in which the edges of the mantle are completely united forward except for a slit for the foot. Such a mantle is said to be closed and is exemplified in Modiolarca, Pandora, Petricola, all pholads, etc. In Fig. 67^4 is shown the unusual condition found in Malletia in which the lower side of the inhalant siphon remains ununited.

The siphons reach their greatest length in extreme burrowing forms and they may remain separate as shown in Tagelus (Fig. 68^5) or lie side by side in a common outer covering as in Mya (Fig. 68^4). They are usually retractile and the muscles which pull them into the shell are attached to the inner side of the valves below the posterior adductor. They are simply the enlarged curtain muscles whose attachment forms the pallial line of the inside of the valves and it is they that form the embayment of the pallial line or "pallial sinus," as it is called. It can, therefore, be determined by the presence or absence of a pallial sinus in a fossil shell whether or not the animal had an open mantle or siphons, and the size of the pallial sinus is an indication of the size of the siphons.

The normal habit of a series of forms, from crawling to deeply burrowing, is shown in the accompanying diagram (Fig. 68) in which are shown the foot, the adductors, the pallial line, and the pallial sinus when developed as well as the siphons. The siphons may be very long as in Mya (Fig. 68^4) and Tagelus (Fig. 68^5). In Ensis (Fig. 68^6), the common razor clam, they are short. The reason is easily understood by anyone who has seen the rapidity with which the razor clam disappears when disturbed. The long, thin shell as well as the shape and anterior position of

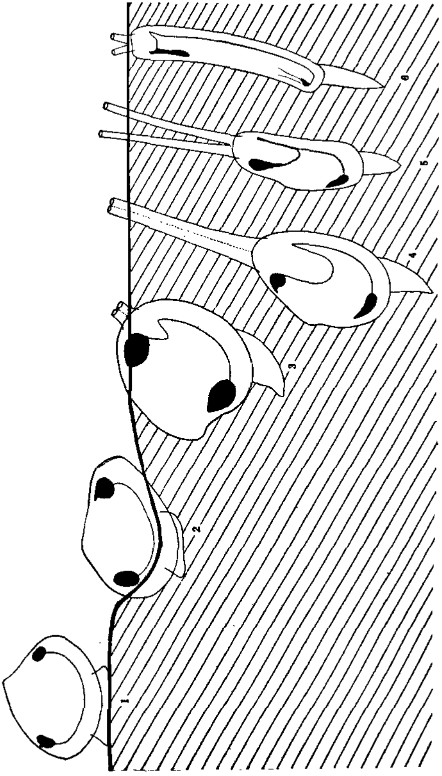


FIG. 68.—Diagrams to scale showing adaptations among the lamellibranchs. 1. Nucula, crawling. 2. Crassatellites, nestling. Different modifications in burrowing forms. 3. Venus. 4. Mya. 5. Tagelus. 6. Ensis.

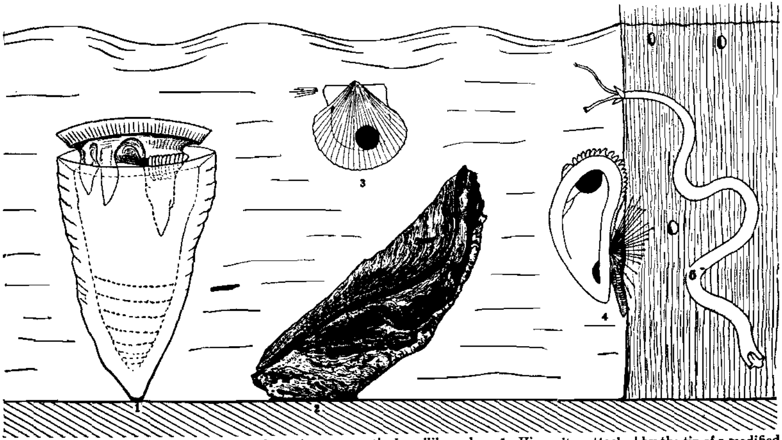


FIG. 69.—Diagrams to scale showing adaptations among the lamellibranchs. 1. *Hippurites* attached by the tip of a modified valve. 2. Ostrea, attached by a but slightly modified part of one of the valves. 3. Pecten, an active swimming form. 4. Mytilus, attached by a byssus. 5. Teredo, the shipworm which bores in wood.

the foot enables it to burrow with great speed; hence, it does not need to be so deeply buried as a Mya to escape its enemies but lies close to the surface, as has been shown; for this reason, its siphons are long enough, and when disturbed it withdraws them and quickly burrows more deeply.

The Byssus.—Many lamellibranchs are provided with a gland on the foot which secretes the horny threads known as a "byssus" by which the animal attaches itself either temporarily or permanently to rocks or other hard submerged objects. Fig. 69^{4} shows a mussel thus attached. This method of anchorage is rather common in the younger forms of various mollusks which may break away, move a short distance, and form a new byssal attachment. Many cease the secretion at maturity and lead a free life. Adult mussels rarely move. On the other hand, some forms, such as the butter shells (Anomia), become firmly fixed for life; Fig. 70^{1} shows the right valve of a young Anomia with the ventral byssus. When this becomes attached, the marg'n of the right valve continues to grow as shown in Fig. 70^{2} until eventually the byssus is completely enclosed and passes through the middle of the valve. It then becomes impregnated with calcite and the animal passes its life lying on its right side and firmly cemented by this calcareous byssal plug (Fig. 70^{3}).

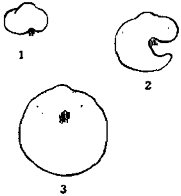


FIG. 70.—Showing the right valve of Anomia from the outside, illustrating the apparent migration of the byssal attachment by the growth of the shell margin around it.

The Gills (Branchia or Ctenidia).—Embryologically, the gills develop from a ridge on either side of the body between the mantle and the foot as a series of filaments which later become more or less united. Existing mollusks are largely classified according to the structure of the gills. In essence, a gill is a stem with a nerve, an artery, and a vein, fringed with two rows of filaments. In more primitive forms the filaments are free from one another and short wide, and flat (Nucula). This type is known as Protobranchia or Aspidobranchia (Fig. $71^{1,4}$). More generally, the filaments are long and slender and bent and are kept from tangling by interlocking patches of cilia or, more rarely, by cross-connections of connective tissue. This type is known as Filibranchia (Fig. $71^{2,5}$). Its logical development is

for each filament to become permanently connected with its fellows and each reflexed end with its main axis (Fig. $71^{2,6}$). These connections give them the appearance of perforated sheets, and this common type is known as "reticulate" or Eulamellibranchia.

A fourth and rarer type is for the gills to be transformed into a muscular partition with a few and larger holes through it, and this type is known as Septibranchia (Fig. $71^{3,7}$).

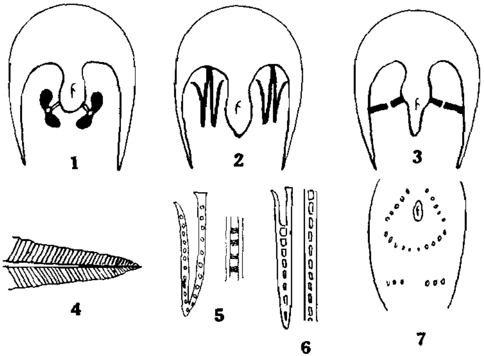


FIG. 71.—Diagrams of gill types in lamellibranchs. Cross-sections of body showing position and form of the gills of 1. *Aspidobranch*. 2. *Filibranch* and eulamellibranch. 3. Septibranch. 4. Side view of an aspidobranch gill. 5. A section and method of preventing tangling of the filaments in a filibranch gill. 6. The same in a eulamellibranch gill. 7. Septibranch viewed from below.

CLASSIFICATION

Various combinations of characters, both of the shell and of the soft parts, have been utilized in classification. Mention has already been made of the use of the adductor muscle scars. In this country many students divide the lamellibranchs into the three orders Prionodesmacea, Anomalodesmacea, and Teleodesmacea, based on the development and character of the hinge, but since the author does not regard either the Prionodesmacea or the Anomalodesmacea as natural divisions, the classification based upon gill structure, although not wholly satisfactory, is

the best that has yet been devised. Below are given the orders and the superfamilies in each:

Order	Name	Superfamilies
Order 1.	Protobranchia	No superfamilies recognized
Order 2.	Filibranchia	1. Anomiacea 2. Arcacea 3. Mytilacea 4. Pectinacea 5. Dimyacea
Order 3.	Eulamellibranchia	1. Ostreacea 2. Submytilacea 3. Tellinacea 4. Veneracea 5. Cardiacea 6. Chamacea 7. Rudistacea 8. Myacea 9. Pholadacea 10. Anatinacea
Order 4.	Septibranchia	No superfamilies

Adaptations.—Some of the normal adaptations for burrowing in the soft sediments of the bottom have already been mentioned. The three principal types of adaptation are (1) the one leading to the extremely wormlike climax of the burrowing type in the shipworm; (2) those forms which live in cavities which they form for themselves in soft rocks or other shells; and (3) an extinct sessile type which became the most modified of all.

In the burrows already described the shells remain of normal shape and size and the siphons become long tubes. There are two families in which the valves remain relatively small and the closed mantle is continued backward as a long pair of united siphons. In the first—the small family Gastrochænidæ—we have a group of diminutive forms in which the hinge teeth are vestigial or absent and the surface of the siphons frequently secretes a shelly lining to the burrow, which may be in soft rock or coral or merely upright in the sand or mud of the bottom. The animal is in no way attached to its tube. Species belonging to this family appear in the Triassic and continue to the present. The second family—the Clavagellidæ—is also small and is found from the Cretaceous to the present. The united siphons secrete a smooth or corrugated tube to the lower end of which one or both valves are soldered. A calcareous disk is secreted in front of the valves by which the whole is attached to some

foreign object and this disk sends out numerous small radial tubes like the spokes of a wheel which assist in holding fast. Neither of these families is of especial geologic importance.

The shipworms belong to the family Teredinidæ, and although they are not of great geological importance, they were tremendously destructive to shipping in the days of wooden vessels, and they still do a large amount of destruction to all submerged wooden structures such as piling, docks, etc. The two equally tiny valves are like a tip on the front end of the body and are no wider than the long siphons, which are united except at their ends, and secrete a shelly lining to the labyrinthine burrow. They fork toward their ends and at the fork there is secreted a pair of tiny calcareous shields (pallets) which close when the ends are pulled in.

In (Fig. 69^5) a Teredo is shown in a timber. Teredos pursue their—from the human point of view—nefarious mode of life, not only in marine water but also in brackish and, in some cases, fresh waters of rivers emptying into the sea. They are found fossil from the Jurassic to the present, and fossil logs, either carbonized, or petrified, completely riddled with Teredo tubes are frequently found fossil in marine sediments.

The pholads (Pholadidæ) range from the late Paleozoic to the present. The shells are thin and ribbed; often the ornamentation differs on different parts of the shell and one, two, or four extra shelly pieces may be fastened to its exterior. The tiny young shell inserts itself in a crevice or depression in submerged rocks, dead shells, or similar objects, and, by churning and rasping with its foot, enlarges the cavity, keeping pace with its growth. A curious adaptive modification serves to support the animal while at work: The valves are held open and pressed against the walls of the cavity. Presumably, the distant pholad ancestor had a functional ligament which served to hold the valves open, but the pholad as we know it has a more efficient method. As the foot grows during adolescence, probably as it did in the ancestral forms, the valves open wider and wider. To prevent the dorsal edges from abrading one another the margins become recurved and the enlarging foot forces the anterior adductor out of the shell onto this recurved shelf, where when it contracts it pulls the shell open. To support the mantle and viscera a calcareous attachment known as a "myophore," which must not be confused with the chondrophore of such a form as Mya, is

secreted. This projects inward from beneath the beaks. When full size is reached, the foot dwindles and a calcareous plate is secreted to close the gap between the mantle edges through which the foot operated during adolescence.

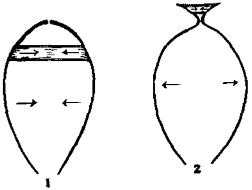


FIG. 72.—Cross-section of valves showing normal position of the anterior adductor, its direction of pull (left), and in the pholads (right) in which the same pull now opens instead of closing the valves.

During the pholad ancestry from the time the anterior adductor migrated outside the valve, the ligament commenced to dwindle and it is rudimentary or obsolete in all known forms.

The most remarkably specialized lamellibranch in the whole history of the race is shown in Fig. 69.[1] This is an extreme adaptation for living attached in an upright position on the bottom in shallow and far from quiet marine waters. This adaptation has so altered the shell that earlier students failed to recognize their nature and most modern students when they first see a specimen are apt to think it is some kind of coral.

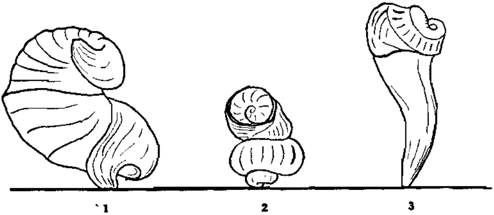


FIG. 73.—Showing the character and unequal development of the two valves in the extinct Mesozoic Diceras (1), Requienia (2), and Caprinula (3).

Beginning with a normally shaped but heavy-shelled ancestor, like the late Paleozoic to Triassic genus Megalodon or the Triassic Carditas, we find a series of attached forms in which the shell thickens to such an extent that the platforms for the adductor muscles and the teeth and their sockets are carried inward a considerable distance, and the beaks of one or both valves become

twisted like a ram's horn, as in the Jurassic genus Diceras (Fig. 73[1]). This gave rise to the family Chamidæ which is a common fossil through the later geological formations and is found in existing seas. All of its other derivatives—and they were exceedingly numerous in the Cretaceous limestone seas of mostly low latitudes—became highly modified and entirely extinct before the close of the Upper Cretaceous. A Lower Cretaceous type (Requienia) in which the attached valve has remained coiled and the free valve, although still coiled, has become flattened and lidlike is shown in Fig. 73.[2] An upper Cretaceous type of Mediterranean Europe and Texas (Caprinula) has the attached valve uncoiled, although the lid valve retains some of its coils (Fig. 73[3]).

The shell walls often became very thick (family Caprinidæ) and developed canals in their substance and the living cavity became much reduced.

In the forms whose exact relationship to the preceding is not clear and which are represented by the two families Hippuritidæ and Radiolitidæ the attached valve was a straight cone which by continued upward growth became cylindrical or columnar, and the upper valve became a thick lid with beveled edges like a manhole cover. The shell substance became extremely thick, lightened, and, at the same time, strengthened by a complex system of canals. The muscles are on internal platforms, and the teeth, no longer on a hinge, are subcentral in position and enlarged to form vertical pegs which fit in the deep sockets of the attached valve. These forms were attached by the apex of the lower valve and as they grew upward to keep free of bottom sediments the animal secreted a succession of floors or stories, living in the last or uppermost. Occasionally, their shells were 2 or 3 feet tall. When the animal opened its shell it simply raised the lid vertically and the teeth were so long that their tips would still be in the sockets. The animals were gregarious like oysters and formed reeflike masses, and it is supposed that the free-swimming larvæ, like the oyster spat, soon attached themselves in the vicinity of or onto their parents.

During the Cretaceous they were widely distributed in the Mediterranean regions of the world in shallow, clear waters whose sediments are generally limestones, and where they occur, they are found in remarkable profusion. For some unknown reason, presumably a result of their great degree of specialization,

they became entirely extinct toward the close of the Upper Cretaceous, due probably to some slight change in their environment to which they could not adapt themselves.

CLASS CEPHALOPODA

The cephalopod class comprise the most highly organized mollusks, one which is unrealizably old, which is represented by fossils in nearly all marine formations, a group that illustrates evolution and adaptation in a way that no other group does, and, what is most interesting, a group which, at different times in different ways, evolves into widely different forms.

Definition.—Bilaterally symmetrical animals (the shells of a few extinct forms are not) with a well-differentiated head provided with prominent eyes, the mouth with jaws and radula. Foot transformed into a ring of appendages (variously termed "lobes," "arms," or "tentacles") surrounding the mouth, prehensile in function, and a muscular tubular organ of two free or united lobes which serves to conduct water in and out of the mantle cavity for respiration and which by violently expelling the water enables the animal to dart backward through the water. This organ is variously termed the "siphon," "funnel," or "hyponomic funnel." The earlier forms were all shelled. Many of the later forms have the shell reduced to an internal vestige or absent entirely. In the living species the gills are either two or four in number. The sexes are distinct and usually somewhat different in size or proportions. The sensory organs are highly developed.

The Cephalopoda are represented in existing seas by four very similar shelled species of Nautilus found in the western tropical Pacific: a single, small squidlike form known as Spirula which has an internal coiled shell and is a pelagic form; several hundred squids and cuttles of all seas in which the ancestral shell is reduced to an internal strengthening axis (pen or cuttle bone); and the less numerous and less active octopus tribe in which every vestige of the ancestral shell has been lost.

Over 10,000 extinct species of great variety of form, and, presumably, of habits, are known. Throughout the greater part of the geological record their representation in the rocks will naturally be the shelled forms, which alone furnish the requisite hard parts for normal preservation as fossils. Among these the great group of ammonites, with their highly specialized septa, have been

entirely extinct since Cretaceous time. The racial history of the ammonite order extended from the late Silurian to the close of the Upper Cretaceous—an inconceivably long period, during which they developed a multitude of forms—and they were easily the dominant cephalopods throughout much of the Mesozoic era.

Since the existing shell-less forms are geologically modern and show every indication of post-Paleozoic evolution culminating in modern times, they afford but slight basis for comparison with the multitude of shelled forms that go back to the oldest fossiliferous rocks. The existing Spirula, which is itself related to the ancestral squids, is quite unlike the remote shelled ancient stock; so that the existing Nautilus alone can serve as a point of departure from which to envisage the structure and habits of the majority of fossil forms. This lack of existing comparable forms has led to serious misinterpretations of extinct forms and has opened the way for a multitude of diverse speculations and generalizations, more often dogmatic than probable.

It would be well to get some idea of the broader features of the geological history of the class before discussing the distinctive features of the three subclasses. This history is summarized in the accompanying diagram (Fig. 74). The oldest ancestral stock which has its last representative in the existing pearly Nautilus starts in the Lower Cambrian, reaches its maximum in the Ordovician and Silurian, and then gradually dwindles, especially in post-Paleozoic times. Its life line is the central one in the diagram.

In the Silurian this stock gave rise to the ammonite line which attained an earlier maximum during the Lower and Middle Triassic and a second maximum in the Jurassic and, dwindling during the later Mesozoic, became extinct in the Upper Cretaceous. This line is shown on the right of the diagram. In the late Paleozoic there diverged from the parent stock a group of active forms in which the shell, always an external and protective external skeleton in nautiloids and ammonoids, was outgrown in youth and at maturity became internal by being enfolded in a pouch in the hinder part of the mantle. This line of descent, known as the "belemnoid," is shown immediately to the left of the Nautilus line in the diagram and in existing seas is represented by the single species of Spirula. The squids and cuttles in which the shell becomes much modified and truly internal have

a geological history dating from the Jurassic. Their line is shown immediately to the left of the belemnoid line. Finally, there is the Cretaceous to Recent line of the entirely shell-less octopus, shown at the left of the diagram.

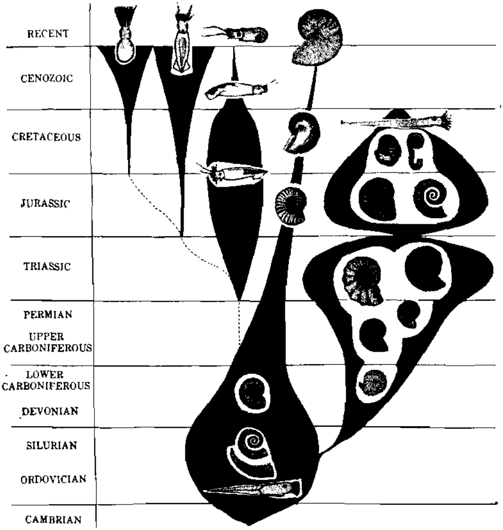


FIG. 74.—Diagram showing the relationships, relative abundance, and geological history of the main groups of Cephalopoda.

SUBCLASS NAUTILOIDEA

This is the most ancient and more primitive group of cephalopods. The shells alone are known except in the single existing genus Nautilus in which the animal is short and stout, with the head much less differentiated than in the squids, with numerous tentacles, and with four gills. The tentacles are not armed with hooks or suckers, there is no ink bag, and the hyponomic funnel

is formed of a right and left part. That the occupants of the host of fossil shells shared all of these features which the Nautilus shows is doubtful but cannot be determined. The shell was always external, and the animal is rather weakly attached to the walls of the living chamber by a pair of lateral muscles at the sides, and these are connected above and below around the periphery by muscular bands (the annulus). The shell, our present chief concern, is a cone which varies from straight through various degrees of coiling. It is coiled in a single plane in the vast majority of nautiloids, but a few have it coiled in an ascending spiral.

The earliest shells are straight, as is the tiny initial part of the shell in the coiled forms. When the newly hatched nautiloid commences its shell it secretes a little horny sac known as the "protoconch" which does not become calcified and so is usually destroyed in fossil forms. With growth it adds onto the rim of the protoconch a flaring saucer-shaped, calcified wall. As it grows, the margins of the shell are built forward and periodically the animal moves forward a slight distance in the shell and secretes a curved partition or floor across the abandoned earlier and smaller portion. These series of partitions or successive floors to the living chamber are known as "septa," so that the shells are said to be septate or camerate. The septa in the nautiloids are usually evenly curved and are complete partitions except that a hole is left open. This is the siphuncle and the edges of the hole are reflected backward to form a calcareous neck or collar; extending backward through this succession of holes is a fleshy cord which is an extension from the visceral cone of the animal and is called the "siphon." It is a remnant from the early days of nautiloid evolution before septal formation had been fully attained and the visceral cone of the animal was larger. The reason that it did not disappear altogether was because it was frequently utilized to secrete horny or calcareous deposits in the unoccupied chambers to counteract their buoyancy and because its retention served to anchor the animal to its shell and, in a measure, made possible the less firm muscular attachment of the animal to the walls of the living chamber—a distinct advantage, since the animal during growth was periodically moving forward in the shell as the margins of the aperture were built forward and new septa were thrown across behind the body.

The lines formed by the junction of the septa with the shell wall are called "sutures," and their form are of the greatest use in the systematic study of fossil cephalopod shells.

The margin of the shell aperture is usually open; that is, the edges are simply the ending of the wall and are not expanded or contracted. When they are inflected and the opening restricted, it means that their owner had habits which differed from the majority of its fellows and demands an explanation. Some of these adaptations as suggested by the unusual forms of apertures are explained in a later section.

The edges are never straight and at right angles to the shell axis. Usually, they are slightly convex at the sides and slightly concave at the top and bottom, and the exact form of the aperture at any stage of the life history of a shell can be made out by noting the course of the growth lines. These convexities and concavities of the edge of the aperture are known as "crests" when they project forward ever so little and "sinuses" when they are embayed. Hence, the normal situation is a dorsal sinus, a lateral crest on either side and a ventral sinus below, often called the "hyponomic sinus," since this part of the shell lies immediately below the hyponomic funnel which the animal uses in breathing and swimming. It has frequently been supposed that the size of this hyponomic sinus shows a relation to the size and power of the hyponomic funnel during life, but this is very doubtful. In the coiled shells the axis of coiling where the whole shell is narrowest is called the "umbilicus." As regards the general form of the shell whether straight or coiled, if it has the appearance of being squeezed from the sides it is said to be compressed and the aperture will be higher than it is wide. If the whole shell is more globosely elliptical when viewed from the edge and the aperture is wider than it is high the shell is said to be depressed.

The shell may be smooth or variously ornamented, less so in nautiloids than in their divergent descendants the ammonoids, and in life it undoubtedly had a color pattern which has usually been lost during fossilization but is preserved in numerous exceptional cases.

Subclass Ammonoidea

The ammonoids, as far as known, were all shelled. The earliest known forms of the Upper Silurian are distinguished

with difficulty from their nautiloid ancestry. The ammonoid line is contrasted with the nautiloids by the tendency of their shells to become ornamented with transverse ribs, tubercles, nodes, or keels. The aperture usually has a ventral crest (rostrum) instead of a sinus. The septa show a tendency to become angular instead of smooth and these inflections of the septa which are especially marked toward the shell wall show their full character in the course of the sutures. The elevations or folds of the septa directed toward the aperture are called "saddles"; the hollows or folds directed away from the aperture are called "lobes"; and both terms apply equally to the sutures.

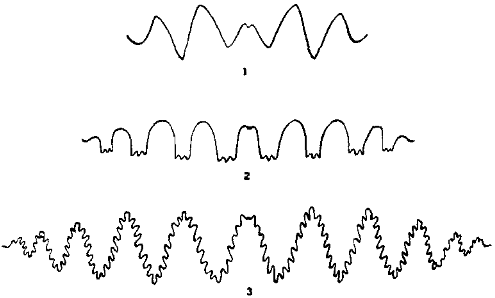


FIG. 75.—Suture of a goniatite (1), a ceratite (2) and an ammonite (3).

The ammonoids show a progressive increase in complexity of the lobes and saddles throughout their history, which is paralleled, to some extent, in the increasing complexity of the successively formed septa during the life history of an individual.

The earliest lobes and saddles are few and angular and characterize what may be called the "first" or "goniatite" stage of racial history (Fig. 75[1]). This passes gradually in late Paleozoic time, but especially in the earlier Mesozoic, into a stage which may be called "ceratitic" and in which the saddles remain smoothly rounded and the lobes develop subordinate small folds (Fig. 75[2]). This is succeeded by the ammonitic or frilled stage in which both the lobes and saddles are folded so that the suture consists of frills (Fig. 75[3]).

The siphuncles are always small and tend to be ventral in position and the siphuncular necks extend forward instead of backward in all but the more primitive forms. The protoconch is calcareous.

Since the ammonoids have been extinct since the Cretaceous, the nature of the character of the soft parts or the habits of the animals can only be inferred.

SUBCLASS COLEOIDEA

This subclass, which includes the remainder of the Cephalopoda, is frequently called the Dibranchiata, since all the numerous existing species have but two gills. They are prevailingly active predaceous forms, with highly organized sense organs. They range in size from less than 1 inch to the gigantic Architeuthis of the North Atlantic which is between 30 and 40 or more feet in length.

They have an ink bag which discharges a sort of smoke screen in the water when they wish to avoid their enemies. The tentacles are few in number—never more than ten—and are armed with hooks or suckers. The shell may be entirely absent (Octopoda) or vestigial (Sepioidea) or only partly reduced (Belemnoidea), but it is never external as in nautiloids and ammonoids except in extreme youth in the belemnoids, where it soon becomes enclosed in a fold of the mantle and is thenceforth internal.

Order Belemnoidea.—The Coleoidea are usually divided into three orders of which the first and most primitive—Belemnoidea—is the only one of any paleontologic importance. The belemnoids appear suddenly in the Triassic, they reach their culmination in the Middle Mesozoic, and gradually die out, but few being known from the Cenozoic, and only the single species of Spirula persisting to the present.

In appearance they resembled a modern squid or cuttle. When hatched the young secrete a straight or loosely coiled shell with regular septa and a siphuncle. When still very small, the soft parts have so outgrown the shell that it becomes buried in the hinderpart of the body, becoming, especially in the family Belemnitidæ, differentiated by growth into three parts—the original septate part known as the "phragmocone"; a shelflike anterior projection of its dorsal margin known as the "proostracum"; and a greater or lesser deposit of calcareous material,

around the apex of the phragmocone, known as the "rostrum" or "guard." This last is the part most frequently preserved in the rocks and has been the basis of numerous ill-defined species.

The second family—the Belemnoteuthidæ—are of little geologic importance and are confined to the older Mesozoic. We would know little about them were it not for the fact that the whole animals are often more or less completely preserved in some of the fine-grained Jurassic muds. They differ from the Belemnitidæ in having the guard or rostrum almost entirely absent so that the internal shell does not differ greatly from the pen of a modern squid.

The third family—Spirulidæ—has the phragmocone loosely coiled—a cyrtocone or gyrocone. In the existing Spirula both the proostracum and the guard are wanting. In the Tertiary genus—Spirulirostra—both the guard and the proostracum are preserved, but they are rare and fragile fossils, seldom met with.

Order Sepioidea.—The Sepioidea comprise the bulk of existing Cephalopoda and include the familiar squids and cuttles. The shell is internal and is not differentiated but consists of an elongated pen, which functions as a stiffening axis for the body and is horny or calcareous. It corresponds to the proostracum part of the shell of the Belemnoidea. The tentacles or arms are ten in number, armed with hooks or suckers, and two of them are longer than the rest.

Order Octopoda.—Body shorter and rounder than the preceding, with eight tentacles, armed with suckers and all the same length. Eyes relatively small and forms mostly inactive. Rarely found fossil.

Evolution of the Cephalopoda

Students are rather generally agreed that the ancestral stock of the cephalopods was essentially like that of all the other mollusks, with a low conical shell, a long creeping foot, and a nearly straight alimentary canal (these parts are shown in black in Fig. 76[1]). Such a form might readily give origin to gastropod, scaphopod, lamellibranch, or amphineuron. To become an incipient cephalopod it would have merely to narrow the aperture of the shell, heighten the cone, and cut off its apex by septa. How this came about will be considered presently.

Figure 76[2] shows a hypothetical stage in which the shell had become partially elongated and contracted; the visceral cone was

correspondingly narrowed; and a few partial septa, lined internally with horny endocones, had developed, much as in the family Endoceratidæ of the Ordovician and Silurian periods, though not in such an advanced manner as in that family. The shell

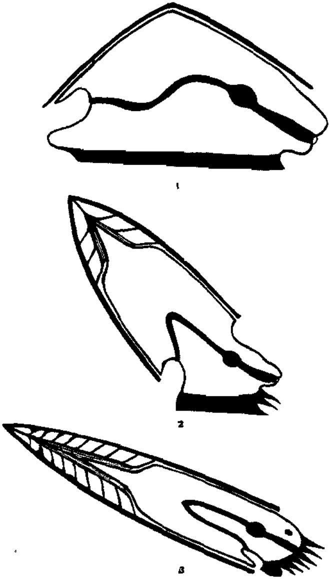


FIG. 76.—Hypothetical ancestral stages leading to a cephalopod.

had not yet developed sufficient air chambers to be appreciably buoyant, and the foot had shortened progressively although still possessing a partially functional crawling surface; its anterior portion had commenced to encircle the mouth and to assume tactile and prehensile functions.

Figure 76^{3} shows a second, more advanced hypothetical stage, with a still narrower and more elongated shell and visceral cone and more numerous septa. The foot is almost completely transformed into tentacular segments, which completely encircle the mouth; its hinder portion had the two reduced lateral halves appressed, much as in the taxodont genus Nucula, and this part became the incipient swimming siphon or hyponomic funnel.

In Fig. 77^{1} we pass from the hypothetical to the oldest known members of the nautiloid line, the actually observed Orthoceras form *with which it is customary to start* cephalopod evolution. The most obvious feature, giving its name to this type, is that the shell is a straight cone (orthocone).

If any single feature can be said to characterize the evolution of the shelled cephalopods as a whole (there are, of course, numerous exceptions due to adaptations to various modes of life), it is that of progressive coiling of the shells.

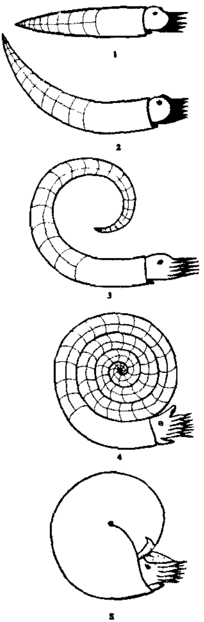


FIG. 77.—Shell form in Orthoceras (1), Cyrtoceros (2), Gyroceras (3), Ophioceras (4), and Nautilus (5).

The first step produces a gently curved or arcuate shell known as a "cyrtocone" (Fig. 77^{2}); the second stage is an incipiently coiled shell in which the whorls are not yet in contact and is known as a "gyrocone" (Fig. 77^{3}); the next stage is one in which the whorls are joined like a coil of rope and is called an "ophiocone" (Fig. 77^{4}). Finally, the side walls of the later whorls pass inward over the earlier whorls forming what is called a "completely involute form," and as it is exemplified in the existing pearly Nautilus, it receives the name of "nautilocone" (Fig. 77^{5}). This, in brief, exemplifies the

normal evolution of nautiloids and ammonoids during millions of years of their history. Why did they become coiled?

The older naturalists, commencing with Buckland in 1835, believed that the early chambers of the shell served for hydrostatic purposes, due, in the first instance, to one of the few mistakes in Owen's account of the anatomy of Nautilus; Owen described the axial canal of the siphon as forming a communicating conduit between the empty chambers and the mantle cavity. When the animal wished to descend, these chambers were filled with water; when it wished to rise, they were emptied—exactly on the operative principle of a submarine. This idea is perpetuated in many books, although the observations on the identical buoyancy in the living and dead Nautilus and the demonstration that the siphon does not communicate with the mantle cavity in Nautilus should set at rest the hydrostatic myth. The earlier and empty chambers in Nautilus are buoyant once for all, and what is true in this respect for Nautilus should apply to all of the extinct forms that did not fill the early chambers with deposits.

This buoyancy of the unfilled earlier chambers is the keynote to the observed changes in shell form, both in the evolution of the race and in the life history of the individual.

With the formation of complete septa shutting off the apical chambers in the developing orthocones, their buoyancy in those forms which did not weight this end by deposits filling the chambers or elaborate deposits about the enlarged siphuncle would tend to tilt the shell forward. Such a tilting would be a handicap in either a swimming or a bottom-dwelling animal. Whether the resulting tension on the ventral side, causing a more rapid growth of the ventral shell margin, or normal secretion of the animal in so orienting its body as to keep its mouth out of the mud of the bottom or to remain horizontal in the water would be the predominant factor cannot be decided. In any event, the more rapid growth on the ventral side would result in an arcuate shell—the cyrtocone—and the more curvature the more the forward migration of the center of gravity would be retarded.

This finally resulted in the gyrocone type of shell. The progressive coiling would not stop with this type, since, as the shell is an expanding cone, the newest chambers immediately behind the living chamber, with their exterior position and much increased volume, would throughout adolescence tend to tilt

the animal forward, and this would eventually result in the coiled type of shell known as an "ophiocone." Complete equilibrium with the animal in a horizontal position most effective for swimming is attained only when the later chambers entirely invest the earlier whorls, as in the existing *Nautilus*—a completely involute form. Or an ophiocone may attain the same stability if there are many volutions to the shell, which serves to explain the persistency of the latter type.

The foregoing simplified series of stages are an epitomy of the general and normal trend of evolution in the shelled cephalopods. The end product would be a nectonic animal with greater or less locomotive powers, as were the majority of shelled forms. But there are a host of exceptions to this general trend as there necessarily must have been if these animals were to adapt themselves fully to the varying environments of the seas—as they undoubtedly did.

In considering these modifications, we may first consider the variations shown in the early orthocones. Fully half of the known Ordovician cephalopods had shells which were orthocones. They have been pictured as swimming in either vertical or horizontal attitudes; as having dragged their horizontal shells over the bottom; as having lived obliquely buried in the bottom; or as having been attached vertically by the apical end.

It has been shown conclusively that some of them were horizontal in their normal attitude. This is proved by the preservation of a well-marked longitudinal color pattern on one side of the shell, which must have been the dorsal, since all marine organisms with a color pattern have the side toward the light contrasted with the opposite side.

If this dorso-ventral color pattern were an isolated case it might possibly be open to doubt, but it has been observed in specimens of orthocones of very different ages and widely separated geographically. Naturally, the preservation of the color pattern of life in fossils of great antiquity is unusual, so that many such instances are not to be expected. Nevertheless, such have been recorded from Ordovician, Silurian, Devonian, and Carboniferous rocks, in both North America and Europe. The author believes such forms to have been swimmers. Some doubtless hovered near the bottom or spent most of their time resting upon it, but others surely must have been more active. The idea that locomotion backward was awkward is wholly anthropomorphic—

it is for us but is decidedly not for a cephalopod. The other idea, that they would run the risk of fracturing the apex of the shell, is altogether fanciful—they did not find their optimum conditions of life on a stern and rock-bound coast, and, in any event, nature by her tendency to overpopulation seems usually to have provided against accidents.

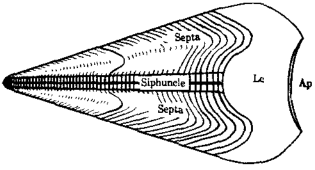
Many students cannot dismiss the idea from their minds that the cephalopod shells were too heavy and too unwieldy to have been propelled by the relatively simple method in vogue among these animals. This idea rests almost entirely upon the handling of museum specimens in which the chambers are filled with lithified sediments or calcified or impregnated or replaced with marcasite, etc. In the vast majority of forms throughout their whole geologic history, the shells were thin and in life were relatively light and easily propelled, and the specific gravity of the whole animal was close to that of the medium—so close, the author imagines, that when the animal was expanded to its maximum extent it would float or rise in the water and when withdrawn within its living chamber it would sink.

A belief in the swimming habits of the majority of orthoconic forms is also a reason for regarding them as having had "arms" like a squid rather than tentacles like a Nautilus, since when swimming these would trail behind and would furnish the necessary rudder to guide their passage through the water more effectively than tentacles. Obviously, all orthoconic forms were not swimmers. Such swimming forms would be expected to show some compression in the cross-profile of the shell, and such is, perhaps, true in a majority of cases. Crawling or groveling forms should show some depression in the cross-profile of the shell, and this can be seen in a number of them.

The extreme example of depressed shell form, undoubtedly indicating a sedentary bottom-dwelling animal which had probably lost the swimming habit and could move only by dragging its shell by the use of its arms, is the genus Gonioceras (Fig. 78). This includes five or six Ordovician species found in Ontario, New York, Illinois, Wisconsin, Minnesota, and northern China. The shell is several times as wide as it is high, with lateral flanges; the septa are closely spaced and sinuous; and the siphuncle is large and nummuloidal. At maturity the aperture is greatly constricted. Since the muscular attachment of the animal to its shell is not especially firm throughout the cephalopoda, this

constriction of the aperture in Gonioceras would serve to prevent the rupture of the muscular attachment when the shell was pulled over the bottom, and the angularity of the septa would also serve to give the animal a firmer hold on its shell.

I have already mentioned the habit of some of the earlier orthocones of using the siphuncle as ballast by secreting a variety of layers of calcite around it or of filling the earlier chambers of the shell to a greater or lesser degree with deposits to counteract their buoyancy. Large and often elaborately ornamented siphuncles occur in a number of families of nautiloids, as, for



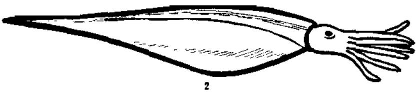


FIG. 78.—The Ordovician bottom-dwelling Gonioceras. 1. Shell from above, showing depressed form, contracted aperture *Ap*, sinuous septa, and heavy siphuncle. *Lc*, living chamber. (*After Ruedemann.*) 2. Restoration of Gonioceras.

example, Endoceratidæ, Piloceratidæ, and Cyrtendoceratidæ; and every degree of internal filling of the earlier chambers may be seen in the families Actinoceratidæ, Jovellanidæ, and Poterioceratidæ—collectively covering the time from Ordovician to Devonian.

An equally effective method of maintaining horizontality is illustrated by the families Ascoceratidæ and Mesoceratidæ—Ordovician and Silurian nautiloids. In these, the shells have advanced slightly beyond the orthoconic form in most of the genera and are more or less cyrtoconic. The living chamber of the adult is long and inflated, often contracted at the aperture, which is sometimes crested. The manner by which the center

of gravity is kept back is by the formation of a linear series of air chambers (saddles) along the dorsal wall of the living chamber. Two examples of this are shown in Fig. 79—Protero-cameroceras (Fig. 79[2]), an orthoconic form, and Ascoceras (Fig. 79[1]), a *cyrtoconic form*. A somewhat similar arrangement is exhibited in the allied family Piloceratidæ of the Ordovician. In Piloceras (*Fig.* 79[3]) *the shell is relatively short and wide; the* animal was stout, its visceral cone extending backward over six-sevenths of the distance to the apex of the shell; the living chamber is restricted dorsally and the animal thus rendered

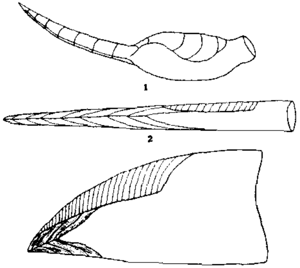


FIG. 79.—Character of the shell in median section in Ascoceras (1), Protero-cameroceras (2) and Piloceras (3).

buoyant by the development of numerous dorsal saddles, and the apex of the shell is ballasted by pseudosepta and conchyolin endocones.

Although what might be called a "normal cyrtocone" was in the line of evolution toward coiled forms, as already indicated, there are a considerable number of forms in the Silurian of small size with short cones (breviconic) that were not of this genealogy and were adopted for a different mode of life. They are all of about the same size, *i.e.*, 4 to 5 centimeters long and 2 to 3.5 centimeters in maximum diameters, and, hence, justly called "small" forms, which are conspicuously marked by mostly transverse color patterns that entirely encircle the shell and prove conclusively that these shells were held erect in life and equally illuminated on all sides. By the same token the animals

were benthonic crawlers and not swimmers. Not only were they crawlers; the author also believes that they crawled by means of a soled foot like that of a gastropod and not by means of their tentacles as does the existing octopus. In fact, were it not for their camerated shells and siphuncles one would be disposed to doubt their cephalopod character and consider them gastropods.

The author's restoration of *Cyrtoceras parvulum* Barrande will indicate sufficiently his conception of the animal (Fig. 80[2]).

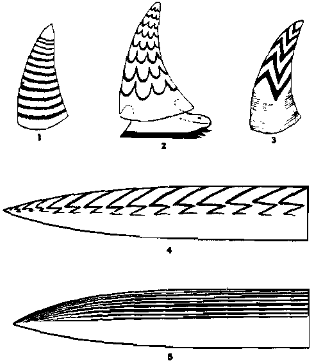


FIG. 80.—Color pattern preserved in fossil nautiloids. 1. Cyrtoceras fallax. 2. Cyrtoceras parvulum. 3. Cyrtoceras decurio. (*After Barrande.*) 4. Orthoceras anguliferum. (*After Dunbar.*) 5. Geisonoceras tenuitextum. (*After Ruedemann.*)

The extent to which the soled foot had assumed a tentacular form in front is, of course, entirely problematic. If these forms were organized as the author has assumed, they would represent a survival, as late as the Silurian, through a continuous ancestry, of the primitive nautiloid organization of the early Cambrian or pre-Cambrian, and otherwise unrelated to their contemporary cyrtoceran associates.

Among these cyrtocones with color patterns on all sides of the shell are *Cyrtoceras fallax* Barrande, with straight transverse parallel bands; *Cyrtoceras zebra* Barrande, with closely spaced fine subparallel wavy bands; *Cyrtoceras intricans* Bar-

rande, with somewhat more angular and less regular bands, more pointed backward than forward and perhaps prenuncial to chevrons; *Cyrtoceras veteranum* Barrande, with closely spaced chevrons; and *Cyrtoceras decurio* Barrande, with large angular chevrons; a sixth species is ornamented with spots all around.

Adaptations for a More or Less Passively Floating Mode of Life.—Adaptations by means of which the animal spent most of its existence in passively floating are various and are attained in unrelated stocks throughout the geological history of the class. Whether they floated near the surface, in intermediate depths, or hanging over the bottom—the feeding ground of the existing Nautilus—is immaterial. Certainly those forms which retained locomotive powers could readily maintain their position at any desired depth. The recurved aperture in such an ammonite as Macroscaphites, or in some species of Heteroceras or Nostoceras, leads to the conclusion that they drifted over the bottom while feeding, but in other genera there is no definite evidence on this point.

FIG. 81.—Restoration of the Silurian Mandaloceras in its floating position.

There are a considerable number of orthoconic Nautiloidea, prevailingly small and breviconic, found from the Ordovician to the Carboniferous and principally in the families Rizoceratidæ, Oncoceratidæ, Poterioceratidæ, and Trimeroceratidæ, represented by a variety of genera and exhibiting numerous differences in their structural details, which floated head downward by reason of the gas-filled chambers of the apex of the cone. This type may be illustrated by Mandaloceras, a Silurian genus (Fig. 81).

In Mandaloceras this position must have been maintained from infancy onward. At maturity the aperture of the living chamber was greatly contracted, but the hyponomic funnel probably retained its propulsive powers since the space in front of it was not roofed over by the inflected margins of the aperture. The expulsion of water from the mantle cavity through the funnel would cause the animal to rise vertically. Many others of these forms had variously contracted apertures leaving only restricted openings for the eyes, tentacles, mouth, and funnel. Some students have thought that this was to be interpreted as indicating that their food was microscopic, and Abel has dubbed

such forms "microphagous." The author sees no reason for limiting the size of their food except by the size of the opening through which it had to pass.

The existing Nautilus is a voracious carnivore, very catholic in its taste. Doubtless, the size of the aperture in such a fossil form as Mandaloceras imposed somewhat narrow limits with respect to size of the food particles, since it could not exsert its jaws and tentacles through so narrow an opening and tear large-sized prey to pieces. The contracted aperture was not, however,

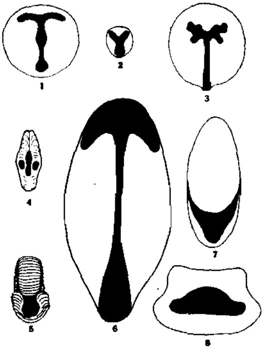


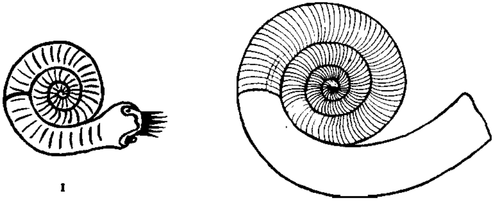
Fig. 82.—Showing contracted apertures in cephalopod shells. 1. Mandaloceras. 2. Ophioceras. 3. Tetrameroceras. 4. Morphoceras. 5. Normannites. 6. Phragmoceras. 7. Arcestes. 8. Hercoceras.

an adaptation due to feeding habits, but exactly the opposite was the case, the contracted aperture having originated as a protective device which also served to keep the animal from becoming dislodged from its living chamber, exactly comparable with the apertures in such land snails as Polygyra, Anostomia, and Pythia. Such a form as Mandaloceras, if its aperture had been an open one, would have been a juicy morsel for its larger and more actively swimming contemporaries (*Fig.* 82).

Many of these early floaters had shells which were cyrtocones, often endogastric, as in the Silurian nautiloid Phragmoceras. These were, in general, somewhat larger forms than the brevi-

conic orthocones like Mandaloceras, but like them they retained the functional hyponomic funnel and had greatly constricted apertures during their adult life. What was said of Mandaloceras applies, also, to forms like Phragmoceras, except that the latter could probably propel themselves horizontally. To rise or sink they would have to depend on the extension or contraction of the arms to induce changes in their specific gravity, unless like the existing Spirula, they could point their funnel in different directions.

Another series of evolutionary changes in the direction of adaptations for floating is exhibited by those nautiloids whose ancestors had completely coiled shells (ophiocones). These may



1 2

FIG. 83.—Showing shell and length and position of the living chamber in Ophioceras (1) and Schrœderoceras (2).

have open apertures, as in Schroederoceras (Fig. 83[2]), an Ordovician genus; or contracted apertures, as in Ophioceras (Fig. 82[2]), a Silurian genus. They are contrasted with such adaptations as Mandaloceras or Phragmoceras in that they were normal swimmers with normally coiled shells during adolescence. At maturity the living chamber became partially free (uncoiled), the margins being built outward to accommodate the growth of the animal, which was then strikingly elongated as compared with the short-bodied Mandaloceras or Phragmoceras and must have passed the remainder of its life suspended obliquely in the water—the weight of the body causing the shell to tilt forward.

The end product of such an evolutionary adaptation as Ophioceras (Fig. 83[1]), in which it is prenuncial, is exhibited by the nautiloid genus Lituites Breyn, which, in early Paleozoic time (Ordovician) set an example of modification that was repeated

in substantially the same way by ammonoid genera like Macroscaphites, eons later. Lituites was a fairly large form in which the first three whorls form an ophiocone, indicative of its ophioconic ancestry as well as its normal swimming attitude during adolescence. After this stage of its ontogeny the diameter of the shell increases rapidly and it is nearly straight in its growth for a distance about fourteen times the diameter of the coiled early portion. The aperture has a shallow hyponomic sinus, narrow ventro-lateral crests, broad lateral sinuses, and fairly well-developed dorso-lateral crests. The living chamber was extraordinarily long and the consequent weight of the animal must have caused the shell to assume an almost vertical attitude in the water. The adult Lituites (Fig. 84) must have drifted, head down, picking up its food on or near the bottom. If the hyponomic funnel remained functional, as the presence of a hyponomic sinus would seem to indicate, it would serve to propel the animal upward, after which the latter would sink slowly. A very slight action of the funnel would serve to keep the animal at any favorable horizon where food happened to be abundant.

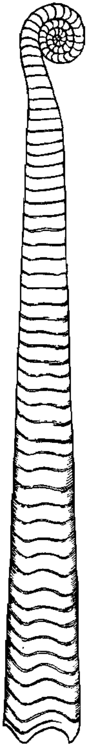


Fig. 84.—The shell of the Ordovician Lituites, one-third life size.

Among the ammonoids, floating adaptations are expressed in various ways. Least modified are various genera of the family Stephanoceratidæ, such as Normannites Munier-Chalmas of the Middle Jurassic, in which the aperture is so contracted that it is difficult to visualize a functional hyponomic funnel, although this is not impossible (Fig. 82[5]). Another involutely coiled small form which seems to have been pelagic is the genus Morphoceras Douvillé of the Jurassic and Cretaceous, in which the adult aperture was almost entirely closed and swimming would seem to have been precluded. It is pictured as planktonic (Fig. 82[4]).

Modified in a different way are those forms which were tightly coiled in their youth but which

have the very long adult living chamber suspended and frequently recurved near the aperture. A good example of this adaptation is furnished by the Lower Cretaceous genus Macroscaphites (Fig. 85[1]) which, like the Ordovician nautiloid Lituites, must have been a swimmer in its youth. At maturity the body chamber hangs down for a distance about equal to the diameter of the coiled disk

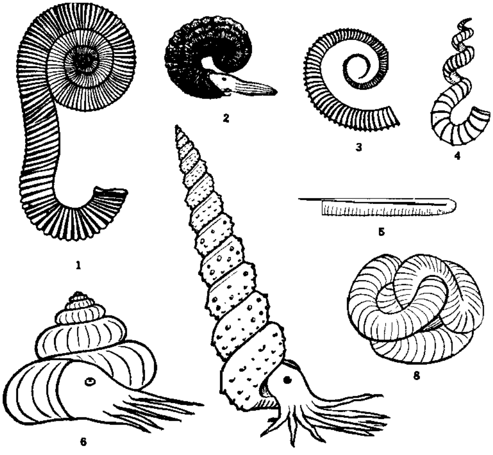


FIG. 85.—Shells of floating, crawling, swimming, and sessile ammonites, all about one-third life size. 1. Macroscaphites. 2. Scaphites. 3. Spiroceras. 4. Heteroceras. 5. Ptychoceras. 6. A low Turrilites. 7. A high Turrilites. 8. The sessile Nipponites.

and finally curves upward at its lower end. The author considers Macroscaphites to have normally drifted, foraging over the bottom, the position of the aperture raising the head above the bottom in an advantageous manner. Possibly the specific gravity was so adjusted that the shell would sink when the animal was withdrawn within the living chamber and rise when it was extended; or when extended and foraging, the funnel, by its action, might either reinforce the induced buoyancy or tilt the

hook-shaped distal end of the shell so that the animal had no difficulty in seizing its prey on the bottom.

The genus Hamites Parkinson, of the Cretaceous, functioned exactly as did Macroscaphites, only in the former genus the early shell was not tightly coiled but was a gyrocone. All of the members of the subfamily Scaphitinæ, as exemplified by the genus Scaphites Parkinson, a world-wide Cretaceous type, were more or less floaters. Indeed, it is difficult to see how the adult of such a species as the Cenomanian *Scaphites æqualis* Sowerby could have swum at all. On the other hand, it is readily conceivable that a form with the aperture oriented as in *Scaphites spiniger* Schluter—a German Upper Cretaceous species—might well have been able to swim (Fig. 85[2]).

Still another type is illustrated by such genera as Spiroceras (Fig. 85[3]) of the Jurassic or Crioceras Leveillé and Ancyloceras d'Orbigny of the Cretaceous. In these the shell is a gyrocone, and such a type might well be a form leading in the direction of Hamites. Another form that appears to the author to indicate a floating existence is such a species of Heteroceras as *Heteroceras reussianum* d'Orbigny (Fig. 85[4]) from the Upper Cretaceous of Germany. This was a relatively small form with a shell coiled in an open ascending spiral, its apertural end recurved as in Macroscaphites, and one which, the author believes, had from infancy the habits described above for the mature Macroscaphites. The genus Heteroceras of d'Orbigny is confined to the Cretaceous period, and all of its species have trochoid spiral shells, but many tend to irregularity, and some appear to have been benthonic rather than pelagic crawlers. Such a form as *Heteroceras stevensoni* appears to the author to have had a crawling rather than a swimming or floating habit.

Such genera as Hamulina d'Orbigny and Ptychoceras d'Orbigny of the older Cretaceous appear to include highly anomalous forms. During growth their shells are relatively slender-chambered orthocones, and, if the earlier chambers contained gas, as there are no reasons for doubting they did, it is impossible to see how they could have been oriented except head downward. At maturity the shell, now much enlarged, bends through an arc of 180 degrees and continues its growth in the opposite direction, the animal this time facing the apex of the shell. This adult enlargement of the body, faced about as it was, would thus shift the center of gravity backward, so that the

animal would now be able to swim in a horizontal position, as has been indicated. In some species of Ptychoceras the living chamber extends farther backward than in the species just figured. For example, in the much smaller Neocomian species, *Ptychoceras emericianus* d'Orbigny (Fig. 85[5]), it extends three-fourths of the distance toward the apex of the shell.

In the genus Ptychoceras the flexed portion is in contact with the earlier part of the shell. Hamulina differs merely in that the two parts do not come into juxtaposition. Hyatt and other authors speak of such forms as these partially uncoiled or secondarily straightened ammonites as "degenerate," but they are obviously not degenerate in any way unless one adopts a creed and considers the closely coiled form of shell the ideal of perfection. Doubtless, the last was an ideal for a swimming habit and that is why such forms predominate in the geological record of the Mesozoic era, but from the point of view of adaptation a Macroscaphites was more specialized and in its adult form would have avoided a certain amount of competition which it suffered in its youth. If cephalopods, or other organisms, can have imputed to them any purposes other than to live and reproduce their kind, then, and then only, is it permissible to speak of modifications such as these as *degenerate.*

Adaptations for a Crawling Benthonic Life.—In considering the mode of life of the swarming ammonites of the Mesozoic and in endeavoring to find some sort of seemingly rational explanation for their remarkably complicated septa, the older naturalists, noting that the growth lines across the venter and the margin of the aperture, when this was preserved, usually showed no trace of a hyponomic sinus such as is present in the majority of the nautiloids, reasoned that there was no hyponomic funnel and, hence, that ammonites as a group were not swimmers but crawlers on the bottom by means of their tentacles and that this habit had induced the development of the lobes and saddles in the septa, since this would enable the animal more effectively to hold and balance its shell while crawling.

This view has been widely accepted, although it is open to insuperable objections. It entirely ignores the meaning of their prevailingly high and often greatly compressed, bilaterally symmetrical, planospiral shells; it ignores the fact that a hyponomic funnel is essential for respiration; it ignores the universal principle of organisms, namely, that a dominant group tends

more or less completely to utilize all available habitats; and it disregards the meaning of wide geographic range which a number of species show.

Narrow planospiral shells fulfil what might be called the "stream-line form" for disks. Many—such, for example, as a large Sphenodiscus—have lines that obviously indicate a movement through the water, and how such high and narrow shells could have been manipulated by a crawling animal is incomprehensible. It is true that there are a number of genera of benthonic gastropods scattered through many families and suborders which have planospiral shells. In the planospiral gastropods the shells are generally small and their apertures wide—usually wider than they are high. None approaches the cephalopod shell form, unless it is the tiny early stage of the genus Cæcum, so that I think it may be conceded that the normally lenticular form of the coiled cephalopods—whether nautiloids or ammonoids—is indicative of a swimming habit.

There are, however, great differences in the transverse profiles of their shells, which doubtless indicate different degrees of resistance to slipping through the water, and, in a general way, ammonites as a whole are more compressed than nautiloids, and the most compressed ammonites, with "cut-water" keels or venters are, in general, among the later forms.

Among the coiled shells of both nautiloids and ammonoids the swimming ability was conditioned not only by the form of the shell and the resistance it offered to passage through the water but also by the power of the hyponomic funnel, and there is no means of obtaining information on this second factor, since the author does not regard the presence or absence of a hyponomic sinus as a reliable indication. This last may, perhaps, be used with caution, but there are forms—Placenticeras, for example—which the author regards as active swimmers, which show no hyponomic sinus.

Transverse profiles of various forms from all horizons show variations from wide ellipticity to extreme compression (Fig. 86). The existing Nautilus, which has a shell almost as blunt prowed as can be imagined and certainly wider than in the majority of fossil forms, is known by observation to swim moderately well, showing how carefully shell form must be used in predicating locomotive ability. Three more depressed and wider forms are shown in the accompanying illustrations—a Polyptychites from

the Lower Cretaceous; a Tropites from the Triassic; and a Cyclolobus from the late Paleozoic, all of which would seem to have been exceedingly poor swimmers. For comparison with these, a profile of Placenticeras, with what the author regards as fast lines,

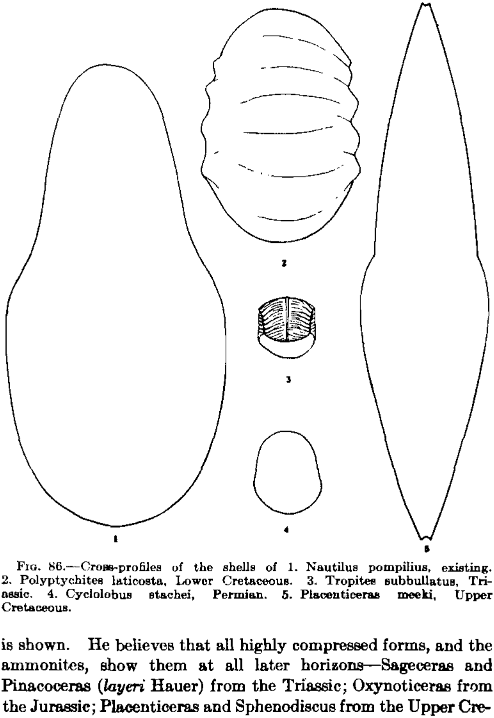


FIG. 86.—Cross-profiles of the shells of 1. Nautilus pompilius, existing. 2. Polyptychites laticosta, Lower Cretaceous. 3. Tropites subbullatus, Triassic. 4. Cyclolobus stachei, Permian. 5. Placenticeras meeki, Upper Cretaceous.

is shown. He believes that all highly compressed forms, and the ammonites, show them at all later horizons—Sageceras and Pinacoceras (*layeri* Hauer) from the Triassic; Oxynoticeras from the Jurassic; Placenticeras and Sphenodiscus from the Upper Cretaceous, etc., were rapid swimmers. Otherwise, their shell form

is meaningless, and it is impossible to imagine the animal as having been able to handle such high and narrow shells in any other way.

There are shell forms, however, both among nautiloids and, more commonly, among the Ammonoids, appearing sporadically throughout all cephalopod history from the Silurian to the Upper Cretaceous, which became secondarily adapted for a benthonic mode of life. All trochoid shells, unless they can be referred to habits of life such as were inferred for *Heteroceras reussianum* (above), may be considered to have led a benthonic existence, and their shells, although much less diversified, may legitimately be compared with those excessively numerous gastropods whose shell plan is an ascending spiral. Instances of a greater degree of reversed adaptation are furnished by the marine limpet-like pulmonates Siphonaria and Gadinia whose ancestors became terrestrial and whose descendents reentered the sea and became benthonic.

That such modifications of the cephalopod shell are not confined to the closing days of ammonite history but occur, also, in the Paleozoic nautiloids is proof that they are adaptations and not degenerations or senile features. As stated, trochoid shells are far more numerous among ammonoids than among nautiloids and among the latter are unknown from horizons earlier than the Upper Silurian (Mitroceras). This is just what might be expected if cephalopod evolution was anything like as outlined. Not only did they take their origin from a benthonic stock, but also it required long ages to acquire the coiled shell. Even as late as the Devonian, 25 per cent of the cephalopods were orthocones and, as has been shown, some of these were benthonic, as were also the breviconic cyrtocones, so that there was no especially untilled field on the sea bottom to tempt the adoption of this mode of life among the nautiloids.

It may also be inferred from the transverse profiles of the shells, although this is highly problematic, that the nautiloid swimmers, as a class, were less effective swimmers than the later ammonoids and fed, for the most part, near the bottom, as does the existing Nautilus. We may also infer that competition for food was keener among the Mesozoic ammonoids than it was among the Paleozoic nautiloids or that the food of the latter was more exclusively nectonic, so that there would have been a greater stimulus for the adoption of a benthonic habit in the Mesozoic

than in the Paleozoic, although this is very hypothetical. Nor can the influeuce of the great abundance of mostly benthonic arthropods in the older Paleozoic (trilobites and meristomes) or of the arthrodiran, ostracoderm, and true fishes be ignored in seeking an evaluation.

Secondarily benthonic nautiloids, descended from coiled swimming ancestors, are the Upper Silurian genus Mitroceras and the Devonian genus Trochoceras Barrande. Among the ammonoids the small *Cochloceratinæ*, as exemplified by such genera as Cochloceras Hauer, or Paracochloceras Mojs., of the marine Triassic, may be mentioned as among the earliest. In the later Mesozoic there are a number of such genera—for example Turrilites Lamarck, Emperoceras Hyatt, Helicoceras d'Orbigny, and probably some species of Heteroceras d'Orbigny—all from rocks of Cretaceous age. The first, especially, often reaches a large size. Two of these secondarily benthonic ammonoids are shown in Figs. 85[6] and 85.[7] Doubtless, the empty early chambers in these forms so reduced their specific gravity that the energy of handling them was reduced to a minimum.

The extreme of benthonic adaptation is that of the apparently sessile, or at least static, genus Nipponites, described by Yabe recently from the Upper Cretaceous of Japan. Nipponites was irregularly coiled like some Vermetus or Serpula—a tendency which may be said to be shown to a very slight degree in certain species of Heteroceras or Nostoceras but which in its extreme development in Nipponites (Fig. 85[8]) is, for the present, highly anomalous but undoubtedly derived from trochoid ancestors, as was the case in the gastropod genus Vermetus.

CHAPTER X

THE PHYLUM ARTHROPODA

The Arthropoda comprise one of the largest and most varied subkingdoms in nature. They are among the most abundant forms in the oldest fossiliferous rocks (Trilobites in the Cambrian); as they are the most abundant forms in modern seas (Crustacea), on the land, and in the air (insects) at the present time. During their long geological history they have diverged quite as much from their ancestral stock and become adapted to a variety of habitats as great as have the vertebrates (fishes, birds, reptiles, mammals).

The accompanying diagram (Fig. 87) illustrates the relations, geological history, and relative abundance of the principal groups. The main features of their evolution may be sketched after enumerating the principal types likely to be familiar to the student. These are the barnacles, crabs, lobsters, crayfish, and shrimps among the Crustacea; the centipedes, the horseshoe crab, the great variety of spiders, scorpions, daddy longlegs, mites, and ticks among the Arachnida; and all the innumerable kinds of insects. The other groups shown in the diagram are, perhaps, strange and it will be the purpose of this discussion to gain some acquaintance with them and fit them into the scheme of evolution.

The name *Arthropoda* was proposed in 1845 and alludes to jointed appendages or legs. Outstanding features of the phylum are the hardened epidermis of horny (chitin) or rarely calcareous material and its division, necessitated by its rigidity, into jointed rings. Thus encased in armor, there is no motion except at the joints, and increase in size can take place only in the short time after the periodic moulting or shedding of the epidermal skeleton (an event known technically as "ecdysis") before the new integument hardens. Each ring (primitively) bears a pair of jointed appendages. Originally, all the joints had appendages and these were similar throughout and locomotor in function, but they have disappeared from some or many of the rings, and those that

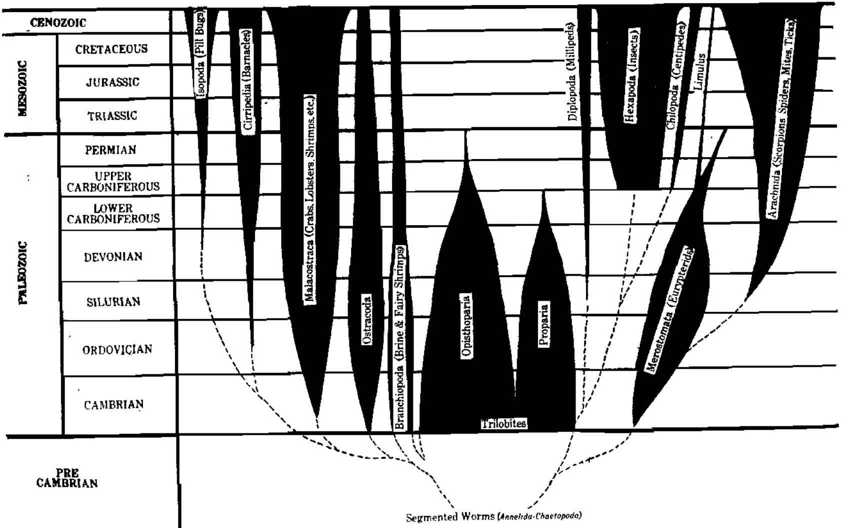


FIG. 87.—Diagram showing the relationships, relative abundance, and geological history of the main groups of Arthropoda.

remain have been modified to perform various functions such as sensation (stalked eyes, feelers), walking, swimming, respiration, copulation, mastication, etc., the one modification shared by all the diverse groups being the utilization of some of the anterior pairs for the seizing and mastication of their food.

In the existing forms in which we can study the anatomy of the internal organs there are other common features, especially in the organization of the nervous and circulatory systems.

The Arthropoda all show evidence of a common derivation from some ancestor much like the existing segmented worms (Annelida Chætopoda). Some of the outstanding features of this evolution are

1. Chitinizing of the integument resulting in the body's becoming encased in a series of rings and the worm appendages (parapodia) retaining their flexibility and usefulness by becoming jointed.

2. The telescoping and consolidation of the anterior segments of the body to form a head, with the consequent consolidation of the ganglia of the segments involved to form a brain.

3. The consolidation of some or many of the remaining segments to form various rigid regions, varying in the different groups according to the habits and increasing their efficiency. Thus, the insects have a solid thorax. Many of the Crustacea and spiders have the head and thorax fused to form a cephalothorax; the spiders have the abdominal segments consolidated; the horseshoe crab has two solid dorsal shields; and the trilobites have a greater or lesser number of posterior segments consolidated to form the pygidium. Throughout the whole phylum in whatever form this consolidation has proceeded it has always moved from free segments to various combinations of fused segments.

4. The modification of the originally similar appendages for special functions such as sensation (antennæ or feelers), stalked eyes of some aquatic forms, jaws, walking or swimming legs, etc., and the elimination of appendages from some of the segments.

5. Transformation of gills into air-breathing organs (lungs and trachea) by means of which the originally aquatic stock was enabled to colonize the land.

6. Development of wings in the insects.

Some of these may now be considered in more detail. Upon examining one of the higher annelids (Chætopoda), a long, slender, many-segmented body will be found. At the front end a head is scarcely differentiated and consists simply of the first segment from which two small tentacles protrude, and at the sides of each body segment there is a lobed appendage known as a "parapodium," prophetic of the arthopod leg.

In the different classes of arthropoda the number of anterior body segments that unite to form the head varies from group to

group, and the efforts of morphologists to find the equivalent number of segments in the head is quite as vain as the attempts to prove that the whole body was of the same number of segments in all the classes. The number of head segments varies from two in the group known as Onychophora (no fossil representative known) to six or seven in the insects. The accompanying diagrams (Fig. 88) in which the internal nervous masses are shown in solid black will make clear the homologies and differences among the principal types.

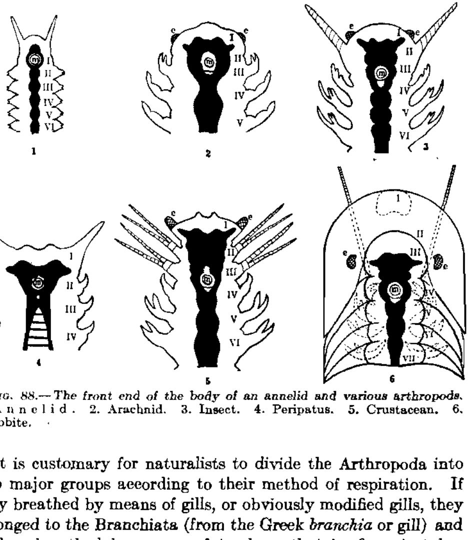


FIG. 88.—*The front end of the body of an annelid and various arthropods.* 1. Annelid. 2. Arachnid. 3. Insect. 4. Peripatus. 5. Crustacean. 6. Trilobite.

It is customary for naturalists to divide the Arthropoda into two major groups according to their method of respiration. If they breathed by means of gills, or obviously modified gills, they belonged to the Branchiata (from the Greek *branchia* or gill) and if they breathed by means of tracheæ, that is, fine air tubes ramifying through the tissues, they belonged to the Tracheata. The method of breathing is purely an adaptive character dependent on whether they lived in water, on land, or in the air, as is shown by the modifications in such terrestrial crustaceans as some of the isopods or the ease with which the book gill of a

Limulus can become a book lung in the terrestrial arachnids or the various means by which the aquatic larvæ of certain insects like the May flies, dragon flies, damosel flies, etc., breathe. These classic but unscientific divisions Branchiata and Tracheata will, therefore, not be used.

TRILOBITA

Trilobites are the most ancient as well as the most primitive arthropods known and when it is remembered that they have been extinct for millions of years it is amazing that we have been able to learn so much about their structure. They were first mentioned in print by Lhwyd in England, iu 1699, and by Guettard in France, in 1757, but that these were not the first to notice them is shown by the finding of a fossil trilobite in a prehistoric human burial, so that it is surmised that a fossil trilobite was part of the bag of tricks of some medicine man of the Stone Age.

In general, they are small, that is, from 1 to 2 inches in length, but there are some groups in which the size is much greater and occasional forms which are veritable giants. These are not restricted to any region or time. Thus, *Paradoxides harlani* of the Middle Cambrian attained a length of 18 inches; *Terataspis grandis* of the Devonian, 19 inches; *Isotelus gigas* of the Ordovician, 17½ inches; *Dalmanites myrmecophorus* of the Devonian, 16 inches; and *Homalonotus major* of the Devonian, 15 inches.

A typical trilobite, such as that shown in the diagram (Fig. 89), has the body divided into three regions. The solid lunate or semicircular front part is the cephalon or head; the midregion of jointed segments is the thorax; and the consolidated tailpiece is the pygidium (not properly an abdomen). Commencing near the front margin of the cephalon is an elevated central axis which extends backward, often to the pygidial border. This axis is bounded by a depression or furrow on each side, thus dividing the body into an axial region in the center and a pleural region on either side, and it was this threefold lengthwise division of the body into an axial and two pleural regions that suggested the name Trilobita which was applied to these animals by Walch in 1771.

The head or cephalon is a solid more or less arched piece, which shows traces of having been formed of several (five to seven) anterior body segments. For descriptive purposes it is con-

sidered to consist of the following parts: The elevated central region is the glabella, showing traces of the original segments of which it is composed in having a frontal lobe, first, second, and third side lobes, occasionally occipital lobes, and an occipital or neck half ring, separated more or less completely from one another by the first, second, and third side furrows and the occipital or neck furrow. In front and on either side of the glabella and firmly attached to it is a gently arched portion termed the "fixed cheeks," and the glabella with the fixed cheeks constitutes what is called the "cranidium." Usually, on either side of the fixed cheeks and marked off from them by what are called the "facial sutures" are the so-called "free cheeks" on the inner margins of which are the eyes. These free cheeks are not free or movable but their union along the facial sutures is not so firm as the other parts of the cephalon so that fossils are frequently found broken apart along the facial sutures, and doubtless the persistence of these sutures was an adaptation to facilitate the periodic moulting habit, the crust of the cephalon splitting along these lines of weakness and disengaging the eyes first. Great importance is attached to the position and course of the facial sutures in the classification of trilobites. Those in which the hinder part (behind the eye) cuts the hind margin of the cephalon constitute the order Ophisthoparia, and those in which it cuts the margin in front of the posterior-lateral or genal angle constitute the order Proparia, and there are good reasons for believing that these two stocks were independent from the time of their origin and that the genal angle in the one order had a different origin from that of the genal angle in the other order. Many trilobites, especially the more primitive, have an elevated ridge (eye ridge) extending sidewise from the glabella and expanding at the margins of the cranidium to form the palpebral or eye lobes which abut against the eyes, these being at the inner margin of the free cheeks.

Most trilobites have fairly large compound eyes, but there are numerous instances where the eyes are lacking and these blind forms can sometimes be shown to have spent their lives burrowing in the mud of the sea bottom and to have been derived from ancestors with normal eyes.

The thorax consists of a few to many (2 to 44) very similar articulating transverse pieces, consisting of the axial part in the center and the pleural part on each side. The pleuræ are usually

furrowed as shown in the diagram but are sometimes smooth (in Illænus, for example).

The pygidium, also frequently and improperly called the abdomen, tail, caudal shield, or plate, is a single, solid, arched, more or less semicircular piece, which usually shows a median axis and a pleural region on either side, and all these usually retain traces of the constituent segments, similar to those of the thorax, of which it is consolidated. The size of the pygidium and the number of constituent segments vary greatly, and in a few forms the former is replaced by a large caudal spine or *telson*.

All of the parts mentioned are shown on the accompanying diagram (Fig. 89). It must not be supposed that the size, proportions, or prominence of these parts are constant. The glabella may be narrow or wide, flat or highly arched. It may extend to or even beyond the anterior border or may be greatly inflated. The eyes vary from small to tremendously large in some instances. The whole body may be highly arched or relatively flat. The elevations and depressions of the surface may be very much accentuated or feebly shown, and some forms are almost smooth. Some forms, also, are highly ornamented in various ways, by the inflation of some of the glabellar lobes or by the development of a tuberculated surface or by developing spiny outgrowths. All of these features reflect the varying habits of the different forms and will be explained under the heading Evolutionary Adaptations.

The features thus far described are entirely those of the hardened epidermal skeleton of the dorsal side of the body which is all that is preserved in the vast majority of fossil specimens. By the painstaking study of microscopic sections and of a relatively few more completely preserved specimens, it has been possible to reconstruct the underside of the animal. That the underside with its appendages is so rarely found is due not only to its more perishable nature but also to the fact that a great many fossil *trilobites are merely the moulted upper hardened surface.* The dorsal crust has an inflected border all around, known as the "doublure," and with this exception the remainder of the underside was covered in life with a thin, unthickened, soft epidermis. This is shown in a median anterior-posterior section in Fig. 90[1].

The soft parts of the animal were of inconsiderable size and were, for the most part, located beneath the arched axis, and

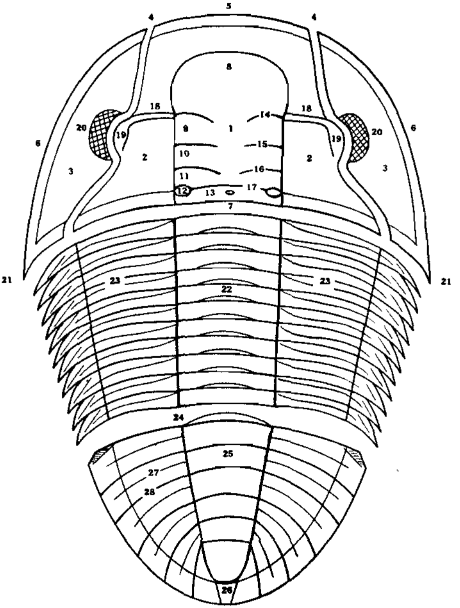


FIG. 89.—Diagrammatic dorsal view of a trilobite showing relations and names of the hard parts. The front division or cephalon is shown slightly separated from the middle region or thorax, and this is slightly separated from the tail shield or pygidium. On the cephalon the following features are shown: The border is differentiated for descriptive purposes into anterior (5); lateral (6); and posterior (7) regions. Within the border and parallel with it is the marginal furrow (not numbered). The free cheeks (3) of the cephalon are slightly separated from the central cranidium which consists of the glabella (1) and a fixed cheek on each side of it (2). This separation is along the facial sutures (4); the part in front of the eye is called the "anterior" or "front branch," and that lying behind the eye is called the "posterior" or "hinder branch." The glabella (1) shows the following features: Elevations: frontal lobe (8); first, second, and third side lobes (9, 10, 11); occipital lobe (12); occipital or neck half ring (13). Depressions: first, second, and third side furrows (14, 15, 16), occipital or neck furrow (17). On the fixed cheeks the ridges running from the glabella to the palpebral or eye lobes (19) are called "eye ridges" (18). The palpebral or

we shall, therefore, look first at a longitudinal section through the center of the axis. Here in heavy black is to be seen the exoskeleton showing, from in front backward, the inflected edge or doublure, the frontal border, and the lobes of the glabella making up the cephalon. Behind the cephalon are the articulating joints of the thorax, and at the hind end the pygidium with its inflected border (doublure). It will be noted that the skin on the underside of the body is not thickened or hardened in

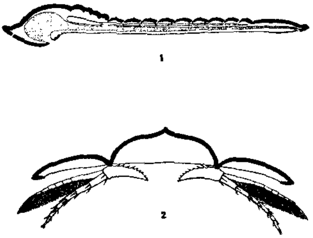


FIG. 90.—1. Longitudinal median section of a trilobite showing exoskeleton solid black), alimentary canal, and heart. 2. Transverse section showing the axis and pleura (solid black) and a pair of appendages.

any way except at the front end. The chitinous plate extending backward from the doublure of the frontal border is known as the "hypostoma" and corresponds to the upper lip of the existing arthropods. Immediately behind it is the mouth which, hence, opens downward and backward. Sometimes behind the mouth a small plate may be present—this is the metastoma. The mouth opens into a short gullet which almost immediately expands into a large stomach occupying much of the central part of the cephalon beneath the frontal lobe of the glabella.

eye lobes (19) lie immediately inside the eyes (20) and are frequently bounded on the inside by the palpebral furrows (not numbered). The posterior lateral or genal angles of the cephalon are frequently produced as genal spines (21). The thorax consists of a central more or less elevated axis bounded on each side by axial furrows and made up of articulating axial rings (22). The parts lying outside the axial furrows are the pleural regions, made up of articulating pleuræ (23), each pleura divided into an anterior and a posterior area by pleural furrows. The pygidium shows a central articular surface (24) at the front end and consists of a rigid central axis (25) bounded by axial furrows and made up of united axial half rings indicated by ring furrows; and rigid side lobes made up of united pleuræ (27) which form ribs (28) where they unite with one another. At the posterior end is a postaxial ridge (26) bounded by postaxial furrows. The side and hind borders constitute the pygidial doublure.

The stomach opens backward into a slender, straight intestine, which continues back to the anus, which is in the pygidium immediately in front of the doublure border. Above the intestine lies the long, many-chambered heart slightly dilated at its front end and tapering backward to the end of the thorax. The digestive glands are at the side of the stomach. No muscles are shown—they are attached to the dorsal crust and must have been essentially similar to those in recent arthropods.

Perhaps sometime it will be possible to say that the size and configuration of the glabella as seen from above will give us a picture of the size of the stomach and, hence, enable us to judge of the nature of the food of particular forms, since a small alimentary tract indicates concentrated food—in the case of trilobites, probably worms—and a large alimentary tract indicates less concentrated food—either vegetable or organic mud which must, therefore, be consumed in much greater quantities. This will enable us to get an idea of the habits of these forms. At present, we know only the alimentary tract, from two or three lucky finds where it was full of mud when the animal died and hardened into rock. We do know, as will be shown presently, that there is the greatest variation in size and form of the glabella, and this, probably, has the meaning that has been suggested but cannot be considered as proved.

The Appendages.—All the segments of the cephalon, thorax, and pygidium may bear a pair of appendages, although only in the genus Neolenus have they been observed on the last or anal segment. The first pair on the head—the antennæ—and the anal pair in Neolenus are simple many-jointed "feelers." All of the intervening ones are much alike and constructed on the same plan—the one which prevails in the simpler existing crustaceans. That is to say, outward from the basal joint (coxopodite) there are two branches, an outer—the exopodite, which may consist of a long basal joint, above which are many small joints, or the basal joint may be long and flat and constitute the whole exopodite. A closely spaced row of long bristles (setæ) extends along the whole hinder edge of the exopodite—and an inner—the endopodite, usually of six joints.

The exopodites were used for swimming and doubtless the fringed margin functioned like gills in oxygenating the blood.

The endopodites were used for crawling. The basal joint to which both were attached articulated on the ridge along either

side of the axis formed by the axial furrows of the dorsal crust, and all of the basal joints were prolonged inward, forming what are known as a "gnathobases"—the gnathobases of the appendages on the cephalon being used for mastication, as in the more specialized mandibles and maxillæ of modern crustaceans, to which they correspond.

A section across the thorax will make these relations clear Fig. 90²: The crust of the axis and pleura is in heavy black. The thin integument of the ventral side is shown stretching from the edges of the doublure of the pleura to the axial ridges and across the axial cavity which contains the heart, intestine, and

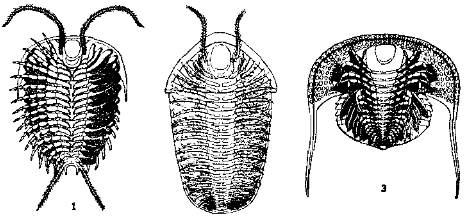


FIG. 91.—Restorations of the underside and appendages of 1. *Neolenus serratus.* 2. *Calymene senaria.* 3. *Cryptolithus tessellatus.* (*After Raymond.*)

principal nerves. The coxopodites with their inwardly directed gnathobases are shown articulating on the axial ridges. The six-jointed spined endopodites are shown below in a leglike position and above them are seen the jointed and marginally fringed exopodites.

Our study of the appendages may be continued by carefully examining the restorations of the lower surface of three quite different trilobites in which the appendages are known. The oldest of these is Neolenus—a Cambrian form (Fig. 91¹). The *antennæ project forward from either side of the hypostoma.* The mouth is to be seen immediately behind the hypostoma and around it are clustered the spiny gnathobases of the four pairs of appendages of the cephalon. The endopodites are omitted on the right side of the drawing so that the fringed exopodites

may be better seen. Note that they consist of a single flattened piece, indicating considerable swimming ability. Note, also, that all the biramous appendages are similar, simply diminishing in size toward the hind end. The anal segment with its central anus is shown bearing two, long, many-jointed tactile appendages corresponding in function to the antennæ on the head. Such tail feelers (caudal rami or cercopods) are present in many of the more simple existing crustacea. They have been discovered only in this one genus of trilobites but were doubtless present in other genera, probably in most forms in which the pygidium remained small or moderate in size. Their delicate nature and the accidents of preservation would easily account for their lack of discovery. We know that all trilobites had antennæ and yet they have been actually observed in less than a dozen genera, and even in these, the majority of specimens fail to show them.

The Calymene (Fig. 91[2]) from the Ordovician may now be compared with Neolenus. The antennæ are shorter, the hypostoma larger, the body margin is not spined, and no tail feelers are known. The balance of the appendages are much as in Neolenus except that the exopodites are not so broad and flat and most of the gnathobases are smooth. Quite differently appearing is Cryptolithus (Fig. 91[3])—an Ordovician form with a very large cephalon and long genal spines, a few-jointed thorax, and a short and wide pygidium. The antennæ are habitually directed backward, as befits an animal that ploughed its way immediately below the surface of the muddy bottoms in search of food. It is surmised that the antennæ would detect the prey which might then be worked forward to the mouth by the action of the gnathobases. The appendages are much as in the preceding genera except that they decrease rapidly in size toward the hind end and each joint of the endopodites has a posterior tubercle and small spines.

The reader should study these drawings carefully, since they illustrate the most striking recent discoveries of trilobite students.

Development.—The earliest stages of trilobite life history, recognized by specimens showing a series of successively smaller stages from the mature forms, with which they are associated, are minute, horny disks about $\frac{1}{25}$ inch in diameter and presumably represent their appearance when just hatched. Such series have been discovered in a considerable number of genera. The newly hatched free-swimming larval trilobite is called a

"protaspis" and corresponds to the first free-swimming stage of the less specialized living Crustacea in which it is called

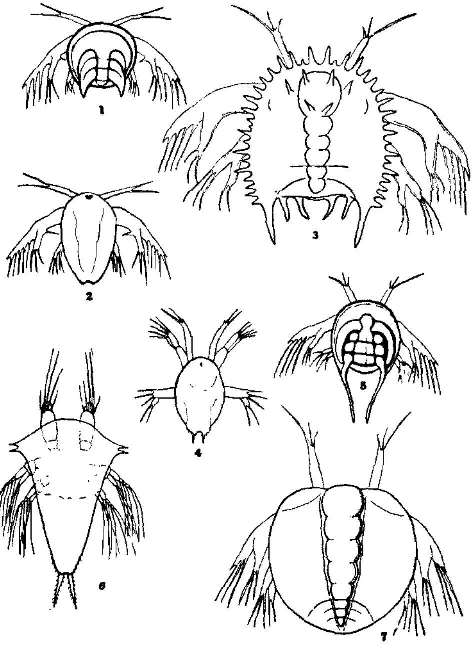


FIG. 92.—Dorsal views of trilobite protaspii and crustacean nauplii. 1. Elliptocephala from Cambrian. (*After Walcott.*) 2. Apus. (*After Claus.*) 3. Acidaspis from the Devonian. 4. Euphasia. (*After Metschnikoff.*) 5. Pædumias from the Cambrian. (*After Walcott.*) 6. Sacculina, a barnacle. (*After Delage.*) 7. Prœtus from the Ordovician.

a "nauplius." Of course, the delicate swimming appendages of the protaspis are not fossilized and these should be added if

it is to have a lifelike appearance. This has been done in the four different protaspis forms figured, (Fig. 92) basing the appendages on those of a modern Apus, and is justified, since all modern nauplii have but three pairs of very similar appendages. Several of these are shown for comparison with the protaspii, each illustrating a different group of Crustacea.

The most primitive protaspii known are shown in Figs. 92^1 and 92^5 representing two Lower Cambrian genera. In both, the protaspis consists of a single dorsal shield with genal spines. The glabella is very prominent and has large palpebral or eye lobes at its sides, although the actual eyes have not been detected. The most interesting feature, however, lies in the traces shown of pleural segments corresponding to the glabellar segments, which is taken to mean a lesser degree of consolidation of the primitive segments that became united to form the cephalon. Figure 92^3 is a much later protaspis from the Devonian the shield of which is rather profusely spined. Figure 92^7 is a smooth protaspis from the Ordovician. In both this one and that from the Devonian, there are indications that the dorsal shield will become divided with additional growth into a large cephalon portion. Note in Fig. 92^3 that the axis is prominent and lobed. From in front backward we see the frontal and first, second, and third glabellar lobes. The furrow which separates the third glabellar lobe from the fourth or occipital half ring is continued outward on each side and will become the neck furrow, so that all but the last lobe of the protaspis axis belong to the adult cephalon. This last lobe and the small central crescent at the side and back of it with four spines represent what will become the adult pygidium. In Fig. 92^7 the axis of the protaspis has eight lobes of which the first five represent the glabella of the adult cephalon and the last three the axis of the pygidium. With each moult, the larval trilobite becomes larger and longer by the addition of free thoracic segments between the cephalon and the pygidium until the adult number and size are attained. These new segments form immediately in front of the pygidium. Contrary to the opinion of several authorities, these new segments do not break off from the front of the pygidium but are formed in front of it, and, in certain cases (*e.g.*, Dechenella and Cyphaspis), where partially detached segments are found at the front of the pygidium, these are believed to be thoracic segments in the process of fusion with the pygidium, thus conforming to

the general rule among all the Arthropoda, in which fusion of originally free segments and not splitting of consolidated parts takes place.

Some protaspii—for example, Dalmanitina—have a distinct pygidium and large marginal eyes, whereas in the adult the eyes are on the dorsal side of the head a considerable distance within the border. Some authors consider this to mean that the evolution of the cephalon commenced with forms in which the eyes and the free cheeks on which they were borne were on the lower side or at the margin of the cephalon.

If it could be shown that all protaspii had marginal or ventral eyes this would not prove such a conclusion, because the majority of adult trilobites were bottom dwellers and the tiny free-swimming larvæ were not, but were nectonic or pelagic, exactly as are the nauplii of bottom-dwelling crustaceans, and the position of the eyes is always adapted to the particular habits of any animal. In describing some of the adaptations of the trilobites in the following section, it will be seen how perfectly the absence or presence of eyes and their size and position are adjusted to their habits of life and particular environment.

Adaptations.—Several thousand different species of trilobites have been described and new forms are constantly being discovered. Many of these are based upon very incomplete specimens, so that it is not possible satisfactorily to explain their adaptations to their various modes of life except in the case of a relatively few forms. All had bilaterally symmetrical depressed bodies and were marine. A general principle of biology indicates that any group of organisms tends to evolve forms adapted to all different environments which are accessible. In the modern world where life is so complex and has become adjusted to competition through long ages, this principle is obscured. In the ancient world this law of adaptation had a more obvious expression. In Cambrian times the trilobites were the lords of creation, they were the dominant organisms of the seas. They had no enemies at first and no serious competitors for food. It is inferred that serious enemies were not present in the Lower and Middle Cambrian, for none of the trilobites of that time are known to have developed the protective device of coiling up like an armadillo with their dorsal armor on the outside of the ball as did practically all the later trilobites. With the evolution of the eurypterids, cephalopods, and, later, the fishes, they had both

enemies and competitors which, in the course of ages, completely exterminated them.

There is every reason to believe that such a varied and vigorous race as were the trilobites exemplified this principle of adaptation and developed carnivorous, omnivorous, and herbivorous forms; forms specialized to various degrees for swimming, crawling, darting, plowing, and burrowing; forms adapted to hard and

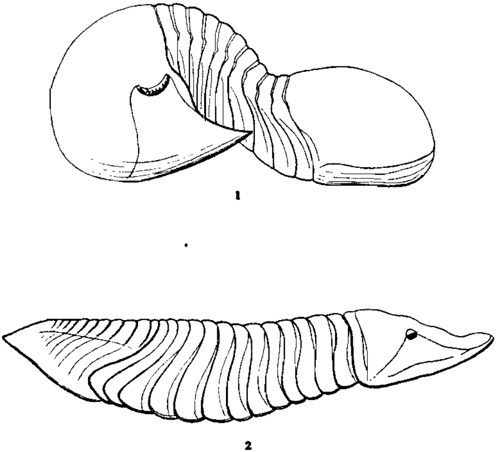


FIG. 93.—Bottom adaptations in two trilobites. (*After Salter.*) 1. Illænus murchisoni. 2. Trimerus delphinocephalus.

soft bottoms, to shallow and deeper waters—in short, adapted to all the environments that are present in the seas and along the continental borders.

It might be expected that some would have ascended the rivers that flowed into the Cambrian estuaries, although this is not certain. Others must have been strand types, judging by similar adaptations which are seen in modern Crustacea, and from such strand and beach-dwelling trilobites it is imagined that later terrestrial arthropods have been derived.

In general, it may be said that the trilobites were poor swimmers; their usually wide and flat bodies and blunt ends were not conducive to great speed but stamp them as more at home on the bottom, as do the normal position of the eyes on the dorsal surface and the finding of their numerous trails and burrows which have been preserved as fossils. These bottom dwellers had habits much like those of the modern horseshoe crab (Limulus) which they greatly resembled in form. Generally speaking, the smaller forms were likely to be better swimmers than the larger. Some of those in which the pygidium became large and approached the cephalon in size and in which it did not assume a peculiar shape and become smooth (adaptations for burrowing

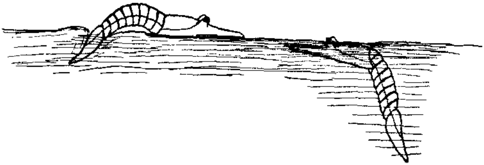


FIG. 94.—*Restoration of Ectenaspis beckeri of the Ordovician, illustrating the* possible habits in Asaphidæ and Illænidæ with smooth, pointed, recurved pygidia and prominent dorsal eyes, as in the genera Vogdesia, Bumastus, Illænus Asaphus, Brachyaspis, etc.

and plowing) are supposed to have been able to dart away from enemies, either forward or backward, by giving a flap to the pygidium after the manner of a modern lobster or crayfish.

Those forms, with a horsboe-shaped cephalon and with the genal spines extending backward over the ends of the pleura, undoubtedly plowed the bottoms in search of food, and such forms tend to have the surface inequalities smoothed out and the eyes high as in Illænus or Harpes, for example (Fig. 93[1]). Others have equally large but less smooth cephalons and use their tail spine (telson) to push themselves along or to right themselves if they accidentally get on their backs, exactly as does a modern Limulus. Other and more sedentary species are modified as in Trimerus (Homalonotus) (Fig. 93[2]), which were rather large and relatively smooth forms with the eyes high up. They probably lay in wait for their passing prey more or less buried in the bottom. A clue to the habits of forms like these was furnished by the lucky find of numerous specimens of

Ectenaspis fossilized in lifelike postures in the original bottom mud. Ectenaspis has the general shape so common in the families Asaphidæ and Illænidæ, with a smooth and pointed pygidium, a flat, snoutlike cephalon, and much elevated eyes. It probably worked its way backward into the soft bottom and lay in wait for its prey with only the eyes above the surface, as shown in Fig. 94.

Another modification is seen in the Ordovician genus Æglina with a much inflated glabella and extraordinarily large eyes so situated that it could see in all directions—up, down, forward, back, and sidewise (Fig. 95). At first glance, such large eyes suggest modern deep-sea animals where the light is very feeble, but this is disproved by always finding the fossils in shallow-water sediments associated with shallow-water organisms. The æglinas are tiny forms and were probably pelagic like modern pteropod mollusks. Possibly, like the pteropods, they were more or less inactive during the day and came out in the late afternoon to feed. This and their open-water life help to explain their enormous eyes.

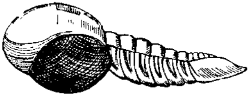


FIG. 95.—The Ordovician pelagic Æglina, four times life size. (*After Barrande.*)

Many trilobites are very much spined—some extravangantly so. It has been the fashion to explain this seeming overornamentation as due to the failing vitality of the race, what the evolutionary philosophers of a quarter of a century ago called "racial senescence." Nothing could be falser or more harmful to a true understanding of the problems of paleontology. The last few millions of years of trilobite history are made up entirely of unornamented types; moreover, there is another and much more probable explanation of the spined forms. The free-swimming larvæ of modern bottom crabs are usually extravagantly spined and it has been observed that the spines increase their buoyancy. They sink much more slowly through the water because of tbe spines on exactly the same principle as snowshoes keep one from sinking in the snow.

This is the clue to some of the spined trilobites, as in Ascidaspis or Albertella, for example. Three different forms of Ascidaspis are figured (Fig. 96) and they are believed to have led a pelagic more or less floating existence. Another type, which from the

position of its eyes and its emaciated body is believed to have led a pelagic life, is the curious little Deiphon of the Silurian (Fig. 97). Spines, in addition, furnish protection to their owners. No predatory animals would care to attack or swallow such prickly balls as a rolled-up Ascidaspis—they were even less vulnerable than a porcupine. Other spines undoubtedly acted

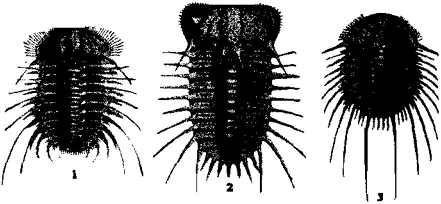


FIG. 96.—Pelagic trilobites of the genus Acidaspis. (*After Barrande.*)

as balancers on the same principle as the balancing rod carried by tight-rope walkers or the manner in which we use our arms in walking a rail.

It seems hardly possible that anyone can look at a Raphiophorous like that shown in Fig. 98, with its long glabellar and two genal spines, without being convinced that they were open-

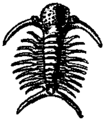


FIG. 97.—The pelagic *Deiphon forbesi* of the Silurian.

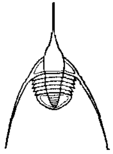
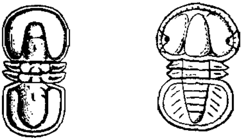


FIG. 98.—The balancing, spined Raphiophorus.

water forms or that when they were enrolled their spines were a protection.

Spines were readily developed as outgrowths of the test, particularly the marginal doublure. An extension of this at any point results in a hollow spine which is all the stronger for being hollow, just as a pipe is stronger than a solid rod of the same diameter.

Quite another problem is furnished by the numerous trilobites which had lost their eyes. This is one of the most important for students of trilobites, since the whole classification of the group is based on what might be called a "philosophy of trilobite evolution," namely, that the more primitive forms had eyes on the lower surface of the head and, hence, that the fossil as it occurred in the rocks would appear eyeless since only the cephalic shield of the top surface would be preserved and that the main course of trilobite evolution was the migration of the eyes to the dorsal surface of the cephalon along with the change from a free-swimming to a bottom-dwelling life. The apparently eyeless forms were grouped by Beecher in an order called Hypoparia an order which is not recognized in this book, since it can be shown that several apparently eyeless forms were descended from normal-eyed ancestors and had actually lost their functional eyes; and also because it can be shown that loss of sight was an adaptation in various lines of evolution which were not actually related and resemble one another only in lacking eyes.



1 2

FIG. 99.—1. *Agnostus montis*, three times life size. 2. *Pagetia clytia*, six times life size, the proparian-eyed ancestor of the blind Agnostidæ.

Among the most aberrant trilobites are those comprising the Agnostidæ, a Cambrian and Ordovician family of tiny forms in which the cephalon and pygidium are the same size and range from smooth to highly ornamental, and in which never more than two thoracic segments are known. The majority show no traces of facial sutures or eyes, and, in fact, most students of trilobites have been unable to determine which was the cephalon and which the pygidium. They have been considered primitive forms by many authors in spite of the fact that throughout the whole arthropod phylum, evolution always proceeds from many to few segments.

The genus Pagetia, described by Walcott in 1916, from the Middle Cambrian of western North America agrees with the typical Agnostidæ in all its features except that it shows typical proparian free cheeks with well-developed eyes at the inner angles of the facial sutures. This almost certainly proves that the

eyeless Agnostidæ were derived from normal-eyed forms, and as a result of living in the dark, buried in the mud of the bottom, the free cheeks coossified with the cranidium and the eyes gradually disappeared (Fig. 99).

The Ordovician trilobites comprising the family Trinucleidæ (Cryptolithidæ) tell the same tale even more conclusively than do the Agnostidæ. They are forms with a large lunate cephalon with long genal spines and with three highly inflated areas in the middle bordered by a broad brim which is conspicuously pitted. The thoracic segments are few in number (five to nine) and the pygidium is small except in the genus Dionide which

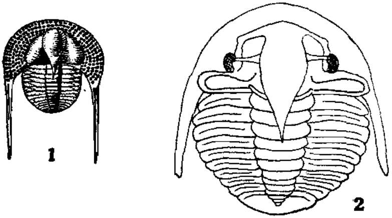


FIG. 100.—1. A blind mud-plowing Cryptolithus (Trinucleus). 2. Orometopus, the opisthoparian-eyed ancestor of the blind Trinucleidæ.

is sometimes segregated as a separate family, although on insufficient grounds. The brim around the inflated part of the cephalon is double, and Beecher and those who follow his views considered this suture along the whole margin to represent the facial suture, although other eminent students of the family point out that it is not the facial suture but an adaptation for ease of moulting. This is rendered probable by the situation in the closely related genus Orometopus with two species in the Ordovician of Scandinavia. In this genus the glabella is inflated, there is a narrow brim around the cephalon, long genal spines, prominent eye lines, and well-developed eyes on normal ophisthoparian free cheeks. Eyes have not been observed in any of the other genera of the family and these eyeless forms are believed to represent adaptations to a burrowing existence and, consequently for living in darkness. During this evolution the brim became greatly extended and highly sensory and was an efficient substitute

for the now useless eyes, the antennæ were directed backward and the free cheeks became coossified with the pygidium to increase its rigidity when pushed through the mud (Fig. 100).

The habit of enrolling to protect the appendages and the soft underside of the animal is an evolutionary trend that develops in all the trilobite lines. Unknown in the early or Middle Cambrian, it appears in various lines before the close of that period and becomes a universal habit in the later forms, which argues that with the multiplication of trilobite enemies during the Ordovician those trilobites which did not develop this protective habit were unable to survive. Two quite diverse types

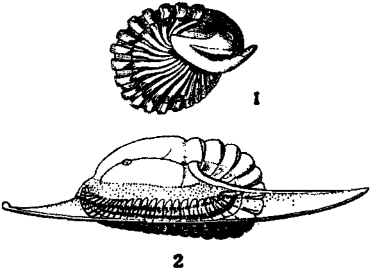


Fig. 101.—Enrolled trilobites. 1. Calymene. 2. Harpes. (*After Richter.*)

of rolled-up trilobites are shown in the figures and this habit was doubly effective in the spined trilobites which somewhat resembled a chestnut burr when rolled up (Fig. 101).

An interesting series of changes is shown in the Lower Cambrian family Mesonacidæ by means of which the adult replaced the hinder appendages and pygidium with a long and powerful spine or telson on the rear of the fourteenth thoracic segment which it utilized as a lever to aid progression through the mud of the bottom, as does a modern Limulus.

The general form characteristic of this family is a large cephalon, semicircular in outline and with genal spines. It is nearly flat and shows no trace of facial sutures. The glabella was narrow in proportion to the breadth of the cephalon. The palpebral lobes are connected with the sides of the glabella and

bear large eyes. The thoracic segments vary from 14 to 44 in number, usually with genal spines, the third segment in the more advanced genera always being much enlarged, and a larger or smaller number of the hindermost segments are usually reduced and terminating in a small, weak, and simple pygidium.

From the central position of the large eyes in all of the forms it is certain that the free cheeks had become consolidated with the cranidium and obliterated the facial sutures in response to the requirements for increased rigidity in mud-grubbing forms. The small, simple pygidium, the large and variable number of segments, and the vestiges of segments in the protaspis are conclusive evidence that the family is not highly specialized. The main evolutionary trend in this family, according to Walcott, is toward the elimination of the wormlike posterior segments of the body carrying the pygidium and the transformation of the fifteenth segment into a large and powerful spine. This is shown in various ways and in the varying degrees in the different genera, which can hardly be regarded as a linear series of stages but as representing steps toward the same end along parallel lines of evolution. The two genera found in slightly older horizons in the Lower Cambrian than the others are Nevadia and Holmia. Nevadia has 28 free segments, the third not enlarged and terminating with a tiny pygidium. None of these develops central spines but the last 11 segments are reduced, their pleura being simple lateral unfurrowed curved spines. Holmia has but 16 free uniform segments and a still smaller pygidium; the third segment is not enlarged, but all the segments except the last two have short median dorsal spines.

The genus Callavia has 15 to 18 free uniform segments, the third not enlarged, and a small pygidium. The segments have short median dorsal spines.

The genus Wanneria is similar without any enlargement of the third segment. There are 16 segments and a small pygidium and the dorsal spine of the fifteenth segment is somewhat enlarged.

The genus Mesonacis shows what might be considered the next step. There are 25 segments in all. The fifteenth is reduced in width and bears a large median dorsal spine. The remaining 10 are spineless, normal in shape but much reduced in size, and are terminated by a small pygidium (Fig. 102^3).

The genus Elliptocephala (Fig. 102^2) has 19 free segments and a small pygidium. The fifteenth to nineteenth are of normal

shape but reduced in size and each has a median dorsal spine, that of the fifteenth being largest.

The genus Pædumias, perhaps, foretells most clearly what the end product of this evolutionary trend was to become. It has from 17 to 44 free segments and a small pygidium. The fifteenth segment is almost completely transformed into a huge spine (Figs. 102[1] and 102[5]) and behind and beneath it there are from 3 to 29 very much reduced and simplified segments ter-

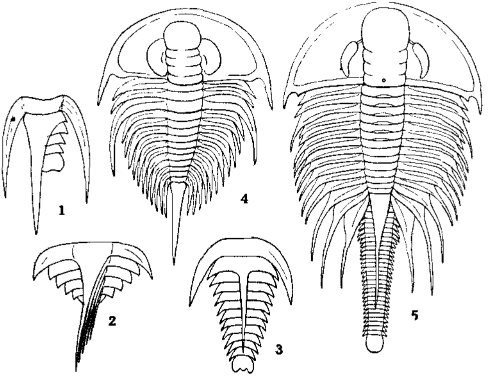


FIG. 102.—Representatives of the Cambrian family Mesonacidæ. (*After Walcott and Burling.*) 1. *Pædumias transitans* (*Walcott*), one and one-third times life size. 2. *Elliptocephala asaphoides* (*Emmons*), life size. 3. *Mesonacis vermontana* (*Hall*), life size. 4. *Olenellus thompsoni* (*Hall*), one-third life size. 5. *Pædumias robsonensis* (*Burling*), one-third life size.

minated by a small, simple pygidium. All that would be necessary now to give us the final form would be for a Pædumias to lose its vermiform appendix altogether at some moult and there would remain, to all intents and purposes, an almost perfect Olenellus.

This genus (Fig. 102[4]), which occurs in the upper part of the Lower Cambrian, will serve to show the general form of all the family. There are 14 normal thoracic segments, the third being greatly enlarged, as in the three preceding genera. The fifteenth segment is transformed into a large, stout spine or telson and the

remaining segments and the pygidium are permanently lost. It is obvious from what has already been said that this telson is not homologous with the pygidium of other trilobites but is a modified fifteenth thoracic segment.

A word of caution is, however, necessary. Some students believe that all of the members of the Mesonacidiæ had a more or less reduced hind end and that those that fail to show this in fossil specimens, such as Olenellus, for example, represent merely incomplete specimens in which this part failed of preservation. This interpretation is quite possible, and if it should be fully demonstrated, then this supposed beautiful evolutionary series just described loses its significance, and all that remains is a clearly discernible evolutionary trend toward a reduction in the number of segments and an adaptational shortening of the body.

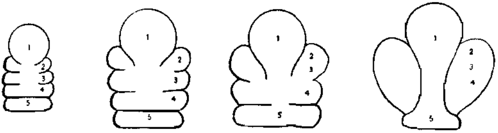
Other evolutionary changes in trilobites which are useful in tracing relationships are the successive modifications of the eye lobes, the changing shape and configuration of the glabella, and the shifting position of the facial sutures.

The primitive eye is on a bean-shaped palpebral lobe connected with the side of the glabella as shown in Olenellus. This evolutionary trend tends to separate the palpebral lobes from the glabella. First, they remain connected by a ridge, as shown in Pædumias, the ridge becomes reduced to a line with the palpebral swelling confined to the end immediately inside the eye proper, and, finally, there remains only the eye swelling with no trace of any connection with the glabella.

The changes in position of the facial sutures are so various in connection with the changes in configuration of the cephalon that they belong more properly under more advanced systematic studies of the trilobites. Their position varies exceedingly. The postocular parts may cut the side borders of the cephalon in front of the genal angles or the posterior border behind the genal angles. In the first case, the genal angles or spines are a part of the fixed cheeks, and in the second case they are a part of the free cheeks, and these two features characterize, respectively, the orders Proparia (meaning "in front of") and Opisthoparia (meaning "behind,") the genal angles, and there are reasons for thinking that the genal angles are not homologous in the two orders but are derived from different original head segments. The preocular part of the facial sutures may shift

even more and sometimes they may go so far as to run together before reaching the anterior border.

The evolutionary changes in the shape and lobing of the glabella are of the greatest importance in tracing relationships and, as has already been suggested, undoubtedly are related to the soft organs beneath, although another factor which complicates our understanding of them is the well-known mechanical principle of increasing the strength of a protective skeleton by arching. A low, flatly arched cephalon is less strong than a highly arched one, and the strength is increased if a number of narrower arches are substituted for a single broad arch. Thus, there are the factors of size and shape of interior organs, the *problem of mechanical efficiency in accordance with the habits*



1 2 3 4

FIG. 103.—Showing the modifications of the glabella in the family Lichadidæ.

of the animal, the necessary mechanical strength to carry the external stresses of the environment, and the internal stresses due to the places of attachment and degree of development of the muscles. It is, therefore, too abstruse for the beginning student but may be profitably illustrated by the changes which take place in the glabella in the family Lichadidæ.

This is an opisthoparian family of considerable size and diversity which was eminently adapted to its environment, for it persisted over the long time interval from the Ordovician to the Lower Carboniferous. The thorax is rather similar throughout, consisting of nine or ten similar segments, but the cephalon undergoes remarkable inflations and both it and the pygidium are highly modified and often elaborately spined. The ancestral form probably had a moderately arched cephalon and a normal glabella like that shown in Fig. 103.[1] The frontal lobe commences to swell, the first side furrows extend backward, cutting off the first side lobes, as shown in Fig. 103.[2] The frontal lobe continues to enlarge, the first and second side lobes swell up and

merge into one and are similarly cut off, and, subsequently, the third side lobe shares the fate of the first two, resulting in a final form like that shown in Fig. 103[4] in which the central and lateral bulbous glabellar lobes may occupy two-thirds of the cephalon and extend forward over the frontal border.

Some of the Devonian forms become elaborately spined as may be seen in the dorsal view of a complete specimen of *Ceratarges armatus* and in the side view of the cephalon *Gaspelichas forillonia* (Fig. 104).

Range.—The trilobites are the only major group of arthropods which are entirely extinct. They range through the whole Paleozoic era, appearing in such abundance in the oldest known Lower Cambrian seas that they must have had a long antecedent evolutionary history. There are over 100 genera and upward of a thousand species known from the Cambrian, the principal families which became extinct before the dawn of Ordovician times being the Eodiscidæ, Conocoryphidæ, Corynexochidæ, Norwoodidæ, Menomonidæ, Burlingidæ, Mesonacidæ, Paradoxidæ, Oryctocephalidæ, and Ellipsocephalidæ. The Mesonacidæ are confined to the Lower and the Paradoxidæ to the Middle Cambrian. The latter contain some of the largest known trilobites.

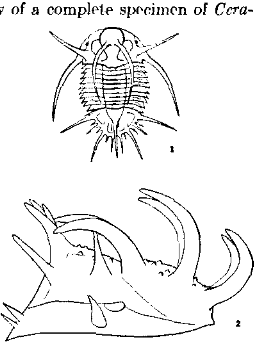


FIG. 104.—1. *Ceratarges armatus.* 2 *Gaspelichas* cephalon. (*After Clarke.*)

Trilobites continued to evolve at a rapid rate during the succeeding Ordovician, from which over 125 genera and about 1,200 species have been described. The rather unimportant families Shumardiidæ, Endymionidæ, Telephidæ, Æglinidæ, Remopleuridæ, Isocolidæ, Holotrachelidæ, Ityophoridæ, Styginidæ, and Cryptolithidæ are confined to the Ordovician, which also witnessed the extinction of the Agnostidæ and the Olenidæ that swarmed in the Cambrian seas, and were on the wane before the dawn of Ordovician time. The families Solenopleuridæ, Ceratopygidæ, Bathyuridæ, Dikelocephalidæ, and Asaphidæ are

all present in the Cambrian; the Dikelocephalidæ, being especially characteristic in the upper Cambrian, became extinct during the Ordovician. Perhaps the most characteristic Ordovician trilobites were the members of the family Asaphidæ.

There is a marked decline of trilobites in the Silurian, since from the close of the Ordovician they are on the wane, at first very slowly, but with terrible speed after Devonian times. There are about 40 genera and 600 species in the Silurian. The families Harpedidæ, Raphiophoridæ, Illænidæ, Goldiidæ, Prœtidæ, Lichadidæ, Odontopleuridæ, Encrinuridæ, Calymenidæ, Cheiruridæ, and Phacopidæ, evolving some time during the Ordovician, continue in the Silurian, and of these the families Raphiophoridæ, Illænidæ, and Encrinuridæ pass on upward into the Devonian. Dominant types in the Silurian and Lower and Middle Devonian are members of the families Prœtidæ, Lichadidæ, Odontopleuridæ, and Phacopidæ. Aside from actual statistics of genera and species, which depend, to a certain extent, on accidents of discovery and varying personal opinions as to what constitutes a genus or species, the fact that no new families were evolved after the Ordovician proves that the group reached its zenith during the older Paleozoic (Cambrian and Ordovician). The Devonian has yielded about 40 genera and less than 200 species. The decline of trilobites is very noticeable during upper Devonian time, and the dawn of the Carboniferous found only the three families Prœtidæ, Lichadidæ, and Odontopleuridæ sparingly represented, and only the single genus Phillipsia of the family Prœtidæ continues into the Permian.

Geographically, the trilobites are found in all of the present continental areas. Some genera, such as Agnostus, Ptychoparia, Paradoxides, Cryptolithus, Illænus, Prœtus, Phillipsia, Acidaspis, Calymene, Homalonotus, Cheirurus, Phacops, Dalmanites, etc., seem to have been truly cosmopolitan, but the majority had a more limited distribution though commonly found in lands adjacent to the present oceanic basins, as, for example, in northern Europe and eastern North America. Northern and central Europe show a remarkable contrast in their Cambro-Ordovician trilobites, as do North and South America in the older Devonian and doubtless, as knowledge is increased it will be possible to understand the provincial trilobite associations and the paths of their dispersal much better than they are understood at present.

Causes of Extinction.—The causes of the decline and fall of the ancient trilobite race can only be surmised. The following may be considered to have been some, at least, of the factors that hastened their end: Structurally they failed to complete a protective exoskeleton, remaining flat and uncompacted and with a defenseless underside. Their appendages remained but slightly differentiated, and they altogether failed to develop special organs for offense and defense like the claws and pincers of the higher Crustacea and the Merostomata. Trilobites may truly be said to have been on a lower plane of specialization both offensive and defensive than the higher Crustacea and Merostomata which replaced them as the scavengers of the seas.

Both of these groups were of later origin, and the Merostomata, which by Silurian time were the dominant forms of life in certain shallow seas, though by no means universally distributed, were dangerous enemies as well as competitors when present. The great evolution of cephalopods, which is so striking a feature of the Ordovician, was also a fatal danger. These cephalopods were largely bottom feeders, so that they not only taxed the food resources of the bottoms but also actively consumed innumerable trilobites. The Silurian seas bristled with enemies, for, in addition to those mentioned, the primitive, depressed, bottom-dwelling fishes (Ostracoderms) were present in the Silurian, and the succeeding Devonian has often been called the "age of fishes."

No mention has been made of such speculative enemies as possible parasites nor the evolving other invertebrate phyla—worms, corals, mollusks, brachiopods, and echinoderms, which were, at least, competitors, and some of the last-mentioned phylum may have been active enemies.

Enough has probably been said to make it clear that, however little is known of the precise causes, the trilobites by Silurian times were in the position of a backward race, out of place amid the host of evolving more efficient creatures and were doomed to extinction.

CLASSIFICATION

The earliest attempt at a classification of trilobites was based on the presence or absence of eyes (Dalman, 1826). Somewhat later, it was proposed to separate them according as they could enroll or not (Milne Edwards, 1840). Barrande, the most

eminent of the earlier students, based his classification on the form and structure of the pleura (1850). The presence or absence of a pygidium was the criterion used by Emmrich (1844). Chapman (1889) based a classification on the features of the glabella. Gurich (1907) devised a scheme based on the number of thoracic segments and the degree of development of the pygidium. The classification proposed by Beecher in 1897 is in almost universal use in America. It was based on a general survey of trilobite structures and on a theory of development of which the critical feature was the relation of the free cheeks to the cranidium. Beecher divided all trilobites into three orders—Hypoparia, Opisthoparia, and Proparia. The Hypoparia included those trilobites which Beecher regarded as most primitive, in which the free cheeks were supposed to form a ventral marginal plate and in which the facial sutures were, therefore, submarginal, marginal, or ventral. Hence, the eyes would be first developed on the ventral side and would, in the course of evolution, pass to a marginal and then to a supramarginal position. This order included six ill-assorted families of mostly blind and unrelated forms and is the portion of Beecher's scheme which has been most severely criticized. The order Hypoparia is not recognized in this book. About the only general feature they have in common is the lack of eyes and in at least two families they can be shown to have been derived from normal-eyed ancestors. All are obviously specialized and not primitive. They find their more natural positions distributed among the families of the other two orders.

The Opisthoparia comprise those forms in which the facial sutures cut the posterior border of the cephalon behind the genal angle, and, consequently, the genal angle or spine is borne on the free cheek and belongs to the ocular segment of the primitive cephalon.

The Proparia include these forms in which the facial sutures cut the lateral border of the cephalon in front of the genal angle, and, consequently, the genal angle or spine belongs to a different primitive head segment, probably the third or fourth glabellar one.

EUCRUSTACEA

The true Crustacea exhibit a much greater range in structural features and habits than do those primitive Crustacea known as trilobites.

They are aquatic and gilled, except for small forms in which the blood gets its oxygen through the general body surface. In all living forms there are two pairs of antennæ, the first pair being known as "antennules." The body is completely segmented (except in certain parasitic forms). The head tends to be united with a variable number of postcephalic segments to form a cephalothorax which frequently secretes a horny carapace and is sometimes strengthened by deposits of carbonate or phosphate of lime. This carapace is bivalved in the ostracods and some other groups, a single piece in the more familiar forms, and of numerous calcareous pieces in the barnacles. The abdomen is usually well developed (greatly reduced in the ostracods). The total number of body segments varies greatly in the simpler forms but is almost constantly 21 in number in the crabs and lobsters. The biramous appendages are much more diversified than in the trilobites and at least three pairs behind the mouth are much modified to serve as jaws (mandibles and the first and second maxillæ). One to three following pairs may also become adapted for feeding, in which case they are known as "maxillipeds." With the exception of certain remarkably well-preserved faunas like that of the Middle Cambrian Burgess shale or the Upper Jurassic lithographic limestones of Solnhofen, the Crustacea are not prominent in the geological record, and with the exception of the Paleozoic Ostracoda they have been very little utilized in geological chronology.

The more primitive forms hatch quickly as a free-swimming nauplius without any trace of segments and with three pairs of swimming appendages which subsequently become the first and second antennæ and mandibles of the adult. This stage is exactly like the protaspis stage of the trilobite. The later stages, acquired by a succession of moults, have no interest for the paleontologist. The more specialized forms develop in eggs attached to the abdominal appendages of the mother and, when hatched, are not greatly different from their parents.

The Eucrustacea may be divided into five superorders—Branchiopoda, Copepoda, Ostracoda, Cirripedia, and Malacostraca. All of these except the Copepoda are found fossil.

Superorder Branchiopoda

The most primitive of these groups—the Branchiopoda—may have a carapace in the form of a dorsal shield, a bivalved

shell, or it may be absent altogether. The body segments are variable in number and the appendages are usually leaflike and lobed, and only rarely are any of them leglike. Usually, there is present a pair of feelers at the end of the abdomen (caudal furci). Branchiopoda inhabit fresh, marine, subsaline, and supersaline waters and are widely distributed.

Four orders—the Anostraca, Notostraca, Conchostraca, and Cladocera—are usually recognized. The last of these—the Cladocera or water fleas, so common in existing fresh waters—are unknown in rocks older than the Pleistocene, but the other three orders (often grouped together as the Phyllopoda) extend back to the Cambrian.

Order Anostraca.—Without a carapace and with a distinct head, stalked eyes present. This order includes small forms from the middle Cambrian (Opabina, Bidentia, Yohoia) and a Tertiary genus, as well as two existing families which occur in saline lakes and brine pools (*Branchipus, Branchinecta, Artemia,* etc.). The geological record of this order is very incomplete.

Order Notostraca.—Carapace present and in the form of a dorsal shield, eyes sessile. The Notostraca are mostly small forms sparingly preserved as fossils but found from the Lower Cambrian to the present. There are at least three Cambrian families. The widely distributed modern family which includes the familiar genus Apus is found as far back as the Permian.

Order Conchostraca.—Carapace present and bivalved, completely enclosing the long body. Eyes sessile. First antennæ minute. Second antennae large. There are 18 to 28 pairs of leaflike appendages, and the abdomen is not bent as it is in the Ostracoda and Cladocera. The Conchostraca have been found as fossils from the Cambrian to the present, being usually represented by only the bivalved carapace, which is distinguished with difficulty from that of the Ostracoda or from minute bivalved molluscan shells.

Superorder Ostracoda

The Ostracoda are present in countless numbers in modern fresh and marine waters and in the past from the Ordovician down to the present. They are frequently found in ancient sediments in such large numbers as to constitute a large part of the rock. With few exceptions, the carapace only is preserved.

This may be smooth and consequently featureless or it may be lobed and ornamented so that species can be used in determining geological horizons.

The *ostracods are all small and many of them are minute* (the largest existing species—the deep-sea Gigantocypris—is a centimeter long). Next to the Copepoda they are the most abundant Crustacea in modern seas. The body is contained within the *bivalved carapace to which it is attached by adductor muscles* which close the valves and sometimes make a scar visible from the outside. The body has become reduced and is indistinctly segmented with seven pairs of appendages (first and second antennæ, mandibles, two pairs of maxillæ, and two pairs of slender legs.) The abdomen is rudimentary and ends in a single or bifurcated spine, used principally for raking out foreign matter that gets between the valves. There is a small median and commonly a pair of larger lateral eyes whose position is sometimes indicated by a pair of eye tubercles on the carapace.

The two valves may be equal or one may be slightly larger than the other overlapping at the top (Bairdia), below (Leperditia), or all around (Cytherella). The relationships of the existing forms rest largely on the anatomy of the soft parts, especially the appendages, and since these are absent in the fossils the paleontologist has to rely on characters of the carapace—its surface ornamentation, the equality or inequality of the valves, the straightness or sinuosity of the dorsal suture, the smooth or spinose character of the margins of the valves, and like features. A great many fossil species have the carapace lobed or nodose, and these doubtless reflect features of the soft body. If the ostracods evolved from the Branchiopoda by a reduction of the body, as seems probable, then a great many of the earlier Paleozoic forms should have had a longer and more distinctly segmented body than the existing forms, and this may account for the persistence of some of the lobes or nodes of the carapace which are common in so many Paleozoic forms. In existing forms, the sexes are distinct, as they undoubtedly were in the past, but their shells are alike, although sometimes one sex may be slightly larger than the other—the males in Candona and the females in Cypris. Certain distinctions in otherwise similar shells, particularly in the extensive Paleozoic family Beyrichiacæ, have suggested sexual differences. This may show in the slightly more inflated hinder part or in a swollen pouch, which has been

called the "brood pouch" and is supposed to indicate a female. The eggs hatch as nauplii.

The body parts of a recent ostracod is shown in Fig. 105,[1] and a few illustrations of the carapace of some Paleozoic genera are shown in Fig. 105[2–13].

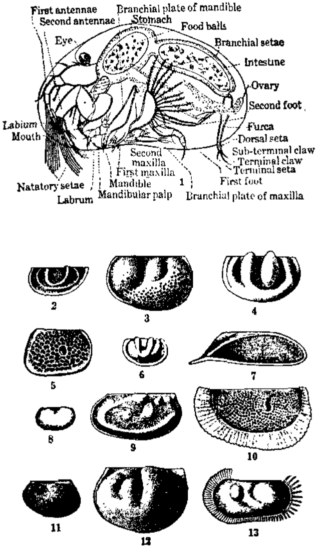


FIG. 105.—A recent ostracod and carapaces of several Paleozoic genera. 1. Body parts of a recent ostracod. (*After Vavra.*) 2. Strepula. 3. Zygobeyrichia. 4. Drepanellina from the Silurian. 5. Kirbya, Devonian. 6. Zygobolba, Silurian. 7. Acanthoscapha, Devonian. 8. Leperditella, Ordovician. 9. Saffordella, Silurian. 10. Eurychilina, Ordovician. 11. Leperditia, Ordovician. 12. Welleria, Silurian. 13. Beyrichiopsis, Carboniferous. (Figures 2 to 13 *after Ulrich and Bassler.*)

SUPERORDER CIRRIPEDIA

The barnacles are always puzzling to the beginner, since the adult acorn barnacle, which is the one most commonly encoun-

tered, looks more like a mollusk than it does like a crustacean and was so considered by such eminent naturalists as Cuvier and Lamarck. It was only after their life history had been worked out, in 1830, that they were demonstrated to be greatly modified crustaceans.

This specialization hinges on their sessile existence and is shown by the frequent union of the sexes in a single individual, by the development of protective plates, and by the simplification of the body with the loss of certain parts. The barnacles are evidently a very ancient group that early became adapted for a sessile life, which suggests that their ancestors were some form of Branchiopoda. The eggs hatch as nauplii which after a succession of moults acquire a bivalved shell like that of an ostracod. They then become attached by their anterior end by means of cement glands emptying on the first antennæ and become transformed into the adult form. This is squat in the acorn barnacles, and stalked in the gooseneck barnacles by the growth of the first antennæ. Somewhat ill understood and questionable forms from rocks as old as the Cambrian have been considered to represent barnacles, but it is not until the Mesozoic that fossils readily comparable with existing forms are found. None are found in fresh water.

The acorn barnacles have from four to ten calcareous plates more or less fused to form a cone, with two pairs of hinged plates known as "scutal" and "tergal," which close the opening when the tide goes out. The gooseneck barnacles have a stalk either flexibly granular or covered with small plates and a variable number of body plates none of which is fused with another. Barnacles are common fossils in the later rocks but are of slight stratigraphic importance.

Superorder Malacostraca

This group contains a great diversity of forms and includes all of the more familiar modern types such as crabs, lobsters, crayfish, shrimps, prawns, etc. It is under only exceptional conditions of fossilization that they are well preserved in the rocks; consequently, they have been rather neglected by paleontologists.

The Malacostraca are the scavengers of the sea bottom, performing in the ocean a task analogous to that performed by the insects on the land. The Recent forms have 14 or 15 body seg-

ments behind the head, paired eyes are usually present and frequently stalked, and, in addition to the appendages on the head, there are eight pairs of thoracic and six pairs of abdominal appendages. Development in the egg is usually carried much farther than in the more primitive Crustacea, so that the newborn are in a postnauplius stage and frequently are not greatly different in appearance from their parents.

The Malacostraca may be separated into a more primitive and a more specialized group. The first or more primitive—the Leptostraca—have the carapace, when present, either sharply folded or actually bivalved, and all of the thoracic segments are distinct. They are mostly small forms, widely distributed in marine waters, and abundantly represented in the Middle Cambrian. The second—the Eumalacostraca—are essentially post-Paleozoic and Recent forms. Their fossil record is too incomplete to give them much paleontologic interest, and they will, therefore, not be described farther than to give an outline of their classification and known geological range.

Syncarida.—This group lacks a carapace and has the first thoracic segment fused with the head.

Order Anaspidacea.—An order found in the Carboniferous and Permian and entirely extinct except for a modern fresh-water Australian form.

Peracarida.—Small and mostly marine forms in which the carapace if present leaves four free thoracic segments.

Order Cumacea.—No fossils.

Order Tanaidacea.—No fossils.

Order Mysidacea (prawns).—Carboniferous to Recent.

Order Isopoda.—Mostly marine but including the terrestrial pill bugs. Devonian to Recent.

Order Amphipoda.—Sand hoppers and sand fleas. Not certainly known before the Teritary.

Eucarida.—Carapace covers consolidated head and thorax, eyes stalked.

Order Euphausiacea.—No fossils.

Order Decapoda.—Here belong the larger and better known existing crustaceans.

Suborder Natantia.—In which abdominal appendages are well developed and used for swimming. Triassic to Recent. Abundant in the Upper Jurassic Solnhofen limestone.

Suborder Reptantia.—Abdominal appendages small, first pair of legs usually enlarged with pincer claws.

Palinura.—Triassic to Recent.

Astacura.—Lobsters and crayfish. Jurassic to Recent.

Anomura.*—*Hermit crabs. Cretaceous to Recent.

Brachyura.—Crabs. Jurassic to Recent.

Hoplocarida.—Carapace small, leaving at least four free thoracic segments.

Order Stomatopoda. A relatively small homogeneous group not certainly known earlier than the later Jurassic but doubtfully reported from the Carboniferous.

CLASS ARACHNIDA

The name is from the Greek for "spider," and the more familiar existing forms are the spiders, scorpions, and ticks, but although fossil spiders are not uncommon as early as the Carboniferous, it is the extinct, scorpion-like aquatic members of the class (eurypterids and their allies) and their sole living descendent—the Limulus—that are most interesting to the paleontologist.

The Arachnida usually have the body consolidated into two general regions, commonly called the "cephalothorax" and the "abdomen." The abdomen is differentiated into a front and hind region in the scorpion, less clearly differentiated in the eurypterids, consolidated in the spiders and limuli, and all segmentation of the body becomes obsolete in the existing ticks and mites.

No true antennæ are known, the corresponding appendages of the arachnids being known as "cheliceræ." None of the appendages around the mouth is greatly modified as jaws, such as are present in the later Crustacea, but all develop gnathobases for crushing food as in the trilobites. The cephalothoracic appendages are, first, cheliceræ; second, pedipalps; third to sixth, legs. None is biramous as in the Crustacea.

The arachnids constitute a distinct line of evolution which diverged probably in pre-Cambrian time from the primitive crustacean stock and early acquired a fixed ground plan of structure. Though far less numerous, they are much more diversified as well as much more ancient than the insects. Respiration is accomplished in various ways—the ancient aquatic forms have leafy gills known as "book gills," the scorpions have much the same organs inverted and known as "book lungs," and the later terrestrial forms have air tubes (tracheæ) similar to those of insects.

The sexes are distinct; the embryo reaches a mature stage before it is hatched; in fact, in the scorpions, mites, and pedipalps, the young are hatched inside the body of the mother. In limulus, spiders and eurypterids, eggs are laid, but the young

when hatched do not differ greatly from their parents, and there are, consequently, no larval stages comparable to those in insects or to the nauplius or other free-swimming larval stages of the Crustacea.

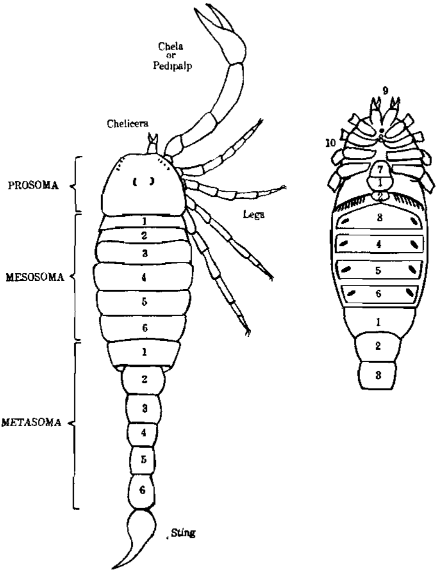


FIG. 106.—Body parts of a scorpion as seen from above and below.

A scorpion is a much better example of Arachnid morphology than any other existing form and we will therefore consider its hard parts in some detail (Fig. 106).

The body may be divided into three regions—a front region to which the legs are attached is the cephalothorax, called the "prosoma" in the arachnids; behind the carapace are seven wide segments; and these are followed by five narrow, ringlike seg-

ments which end in the sting. If a specimen or the accompanying diagram is examined, you will see that the first six segments behind the carapace consist of dorsal pieces (tergites) and ventral pieces (sternites) the lateral edges of which are separated by soft skin. The first has the genital opening on the underside covered by a lid or operculum, and the second bears a pair of comblike appendages (pectens) which are tactile organs. The third to the sixth have broad, flat, sternal plates with oblique slits near each margin known as "stigmata" and serving to admit air to the body.

These six segments behind the carapace constitute the second body region known as the "mesosoma," also often called "preabdomen." The seventh to twelfth segments comprise the "metasoma" (postabdomen or tail). Although the seventh segment is wide like the preceding ones, it lacks stigmata and has its tergite and sternite more or less united so that it is grouped with the ringlike eighth to twelfth segments. The sting is considered an appendage of the twelfth segment. It consists of a swollen base (vesicle), containing a poisonous fluid, and the spined end (aculeus). The carapace carries two large median eyes and simple eyes at the sides of the front margin. The appendages from front to back are the cheliceræ which are three jointed and correspond to the antennæ of Crustacea. Next, the large pincer-ending chelæ or pedipalps, followed by four pairs of seven-jointed legs with three terminal claws. The bases of the first two legs and those of the cheliceræ and chelæ are arranged about the minute mouth. Between the last two leg bases is a small central plate or sternite. The first segment of the mesosoma carries the genital opening which is covered by a conspicuous operculum. The operculum, which is sometimes elaborate in the eurypterids, is considered to represent a pair of fused appendages. The second segment of the mesosoma shows a small central sternite and carries a pair of comblike appendages which is believed to represent a survival from the aquatic gilled ancestral stage, this first pair of mesosomatic gills having persisted with its form scarcely modified as a sensory organ used in copulation.

The Arachnida are generally divided into two subclasses—the Merostomata and the Embolobranchiata—based primarily on their adaptation to an aquatic or terrestrial environment. Thus, the Merostomata, the more primitive of the two, were aquatic

and consequently breathed by means of gills and lacked malpighian tubes and salivary glands which were necessary in the terrestrial subclass in which the gills became replaced by lungs or air tubes.

Subclass Merostomata

The Merostomata, sometimes called the Gigantostraca, since they included the largest known arachnids, appear in the geological record certainly as early as the Cambrian and doubtfully in the late pre-Cambrian. They are locally abundant throughout the older Paleozoic and, except for a single one of the four orders into which they are divided, become extinct during the Paleozoic. Many students consider that the arachnids, trilobites, and true crustaceans represent three divergent lines of descent from a common pre-Cambrian ancestor. Others think that the trilobites represent this common ancestral stock, and much can be said in favor of this second hypothesis.

The Merostomata are usually subdivided into four orders—Eurypterida, Xiphosura, Synxiphosura, and Limulava. The last, based upon the two crustacean-like genera Sidneyia and Amiella from the Middle Cambrian, is of doubtful validity and probably should not be recognized.

Order Eurypterida.—The eurypterids are among the most primitive known arachnids and are one of the most interesting known groups of fossil organisms. They have elongated bodies with a prosoma like that of a scorpion, carrying a pair of bean-shaped eyes and usually an additional pair of eye spots (ocelli), and six pairs of appendages. The mesosoma consists of six free segments carrying five pairs of small, leaflike appendages. The metasoma consists of six articulating, gradually tapering segments terminated by a telson, which may be a long spine or a short, flat plate. The carapace is thin and is characteristically ornamented with fine scales or tubercles.

The Eurypterida include the largest known arthropods, both Pterygotus and Styloneurus sometimes reaching a length of nearly 10 feet. They are clearly aquatic and mostly bottom dwellers, but there has been much difference of opinion among naturalists as to whether they normally dwelt in marine or fresh waters because of their local occurrence and associates in the rocks. One view would have them originating in rivers and subsequently becoming adapted to living in coastal lagoons, and

the other view believes the reverse to have been true. Certainly, the most famous fossiliferous localities appear to represent coastal lagoon environments. When hatched, the eurypterid is much like the adult in form, differing only in minor particulars such as the relatively large carapace and eyes, a somewhat fewer number of free segments (9 or 10 instead of 12), and a less marked differentiation between mesosoma and metasoma. Three of these young are shown in Fig. 107.

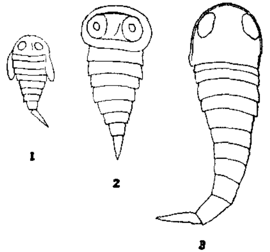


FIG. 107.—Young of (1) *Euryplus maria*, twice life size; (2) *Styloneurus myops*, ten times life size; and (3) *Hughmilleria shawangunk*, ten times life size. (*After Ruedemann.*)

The oldest certainly identified eurypterid is Strabops from the Upper Cambrian. It is about 2¼ inches long with a small prosoma and small eyes. The 12 free segments are not differentiated into mesosoma and metasoma in appearance, although probably the gill plates were confined to the mesosoma as in later forms. The telson is short, broad, and pointed. Strabops looks much like the newly hatched later forms.

The general relations and geologic history of the principal genera are shown in the diagram (Fig. 108), and it will be seen that an unknown interval covering two-thirds of the Ordovician period intervenes between Strabops and the seven genera which appear in the late Ordovician. Most of the genera were short lived, so far as we know the record, but the latter is so incomplete that it may be misleading. The three long-lived genera are Pterygotus, which ranges from late Ordovician to early Devonian and reaches its maximum in the late Silurian; Eurypterus, which

ranges from late Ordovician to Permian and reaches its largest size and greatest abundance in the late Silurian; and Styloneurus, which ranges from late Ordovician to early Carboniferous and also reaches its maximum in the late Silurian.

In this respect, also, the known record may be faulty, for it does not seem probable that the time of actual greatest abundance of these three quite different genera should coincide with the time when, both in North America and in Europe, eurypterid fossils are most frequently and best preserved, for most of the good specimens come from three or four localities and clearly represent accidents of preservation and discovery.

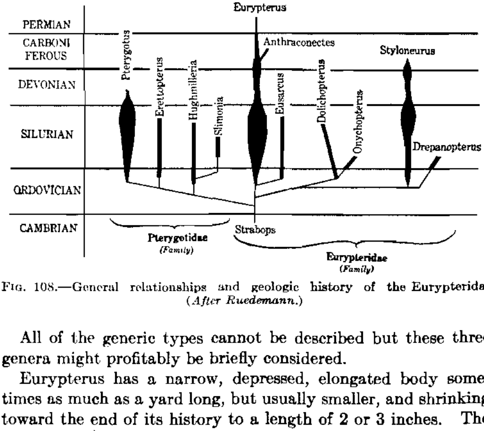


FIG. 108.—General relationships and geologic history of the Eurypterida. (*After Ruedemann.*)

All of the generic types cannot be described but these three genera might profitably be briefly considered.

Eurypterus has a narrow, depressed, elongated body sometimes as much as a yard long, but usually smaller, and shrinking toward the end of its history to a length of 2 or 3 inches. The chelicerae are short and do not project beyond the front border of the carapace. They are followed by five pairs of legs which increase in size from front to rear, a feature true of the whole order except the genus Eusarcus, in which the reverse is the case. The second, third, and fourth pairs are six to eight jointed and finely spined; the fifth pair is eight jointed and spineless; and the sixth pair, very large, powerful, and flattened, are frequently called "paddles" and were used for swimming or

FIG. 109.—Relative sizes and habits of the Eurypterids. (*After Ruedemann.*) 1. The swimming Dolichopterus. 2. Eurypterus. 3. Pterygotus. 4. Hughmilleria. 5. Eusarcus. 6. Stylonеurus. 7. Eurypterus. All about one-fifteenth life size.

moving over muddy bottoms. The eyes are large and on the upper surface of the prosoma just in front of its middle. The female genital appendage consists of several lobes, and the telson is long and spinelike.

Pterygotus has a still narrower body; the large eyes are marginal; the telson is flat, short, and rounded; the cheliceræ are extremely long, longer than any of the other appendages though comprising but three joints. The female genital appendage is simple. Pterygotus commonly grew to a length of several feet and rivals Styloneurus for the distinction of being the largest known arthropod.

Styloneurus has its eyes on the central dome of the carapace; *a long, slender spine of a telson; short cheliceræ; enormously* elongated legs, the last pair being nine jointed and about as long as the body.

The eurypterids must have been sluggish animals and poor swimmers. From the shape of the body, character of the appendages, and position of the eyes we can infer something of their habits. The majority lay partially buried on soft bottoms waiting for their prey. Thus, Eusarcus was a good walker and an especially poor swimmer; Dolichopterus was an unusually good swimmer for a eurypterid; Pterygotus waited for its prey masked in the bottom mud and then seized it with its long pincer-like cheliceræ. The relative size and habits of the more important genera are shown in the accompanying restoration (Fig. 109).

Order Xiphosura.—The name, derived from the two Greek words meaning "sword" and "tail," refers to the long, slender telson. The body is more or less longitudinally three lobed. Cephalothorax large and semicircular. Abdomen of seven to ten segments, variously free or united, the six anterior carrying the genital operculum and the book gills. The order includes a considerable number of imperfectly known genera (Cyclus, Belinurus, Euproöps, Protolimulus, Prolimulus, Prestwichianella, and Paleolimulus) from the Devonian, Carboniferous, and Permian; and the well-known genus Limulus which has at least six Triassic species, and which is represented in existing coastal waters from Maine to the Gulf of Mexico and along the eastern coast of Asia from Sumatra to Japan.

Limulus has the exoskeleton of the body consolidated into two principal regions, an adaption induced by the habits of the

animal, which spends most of its time in plowing over the soft surface of the sea bottom in search of food (principally worms), much as did numerous genera of trilobites. This habit has induced the rosette of flat plates on the hind legs; the consolidation of the abdominal segments; the telson, which is used both for propulsion and to enable the animal to right itself when it happens to become overturned; and the lidlike operculum and gill covers to prevent the fouling of the gills by mud. The muscles between the cephalothorax and the consolidated abdomen and between the abdomen and the telson are powerfully developed.

The cephalothorax or prosoma is semicircular, with strongly developed genal angles. It consists of at least six segments (probably more), carries seven pairs of appendages on its underside, and bears two large compound laterally directed eyes at the edges of the most elevated central part and a pair of eyespots (ocelli) near its frontal border. The appendages are, from in front backward, one pair of cheliceræ, which are small and three jointed; five pairs of essentially similar strong legs, the basal joint of each with gnathobases—spined on the first four and with a cutting edge on the fifth—arranged around the slitlike mouth. The seventh pair of appendages which lie behind the mouth and correspond to the sternum of a scorpion are flat-spined processes known as "chilaria." The legs are essentially similar, with pincers (chelæ) at ends (except second or second or third on male, which are clawed) and are six jointed (the fourth joint consisting of two joints fused) instead of seven, as in the scorpion. The last pair of legs is provided with a rosette of flat plates at the end of the fourth joint to aid in crawling over soft bottoms.

The mesosoma and metasoma are not visibly differentiated and are covered by what is sometimes called the "posterior carapace." The former is distinguished in dorsal view by its marginal spines and in ventral view by its appendages and is taken to include the seventh to twelfth body segments, which are distinct in some of the earlier allies of Limulus. Viewed from below, the most striking feature of the mesosoma is the large genital operculum of its first segment. This practically covers the remaining appendages, which consist of five pairs of medianly fused plates each covering book gills. The metasoma is consolidated with the mesosoma and is considered to represent the thirteenth to eighteenth body segments.

Little need be said of the anatomy of Limulus. In the diagram of the side view, the outlines of cephalothorax, abdomen, and telson are shown as well as the position of the eye and the appendages and the outline of the alimentary canal and above it the

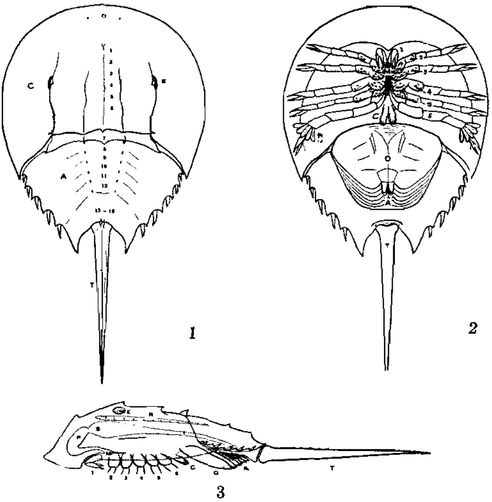


FIG. 110.—Upper (1), lower (2), and median longitudinal section (3) o *Limulus.* The upper view shows united body segments 1 to 18: *o*, ocelli; *E*, eyes; *C*, carapace, prosoma, or cephalothorax; *A*, abdominal carapace; *T*, telson. The lower view shows appendages 1 to 6 around the mouth: *M*; *C*, chilaria; *O*, operculum; *A*, book gills. 5. Telson. *P*, rosette of plates on the hindermost legs. The section shows 1 to 6 bases of appendages. *C*, Chilaria; *M*, mouth; *P*, anterior stomach; *S*, stomach; *I*, intestine; *E*, eye; *R*, heart; *O*, operculum; *A*, book gills; *T*, telson.

tubular heart. The other systems of organs as well as the details are necessarily ignored.

Order Synxiphosura.—A little-known group in which the mesosoma and metosoma have free segments. Includes the single middle Cambrian family Aglaspidæ and the Silurian genera

Neolimulus, Bunodes, Hemiaspis, Bunodella, Pseudoniscus, and Bunaia, all of which are too imperfectly known to determine their relationships with one another or with the other orders of the subclass Merostomata.

Subclass Embolobranchiata

The Merostomata, so far as known, were wholly aquatic. The Embolobranchiata are prevailingly and, perhaps, wholly terrestrial, although some of their earliest representatives may have been aquatic. A terrestrial life demands important adjustments and adaptations for any organism except the smaller and more simple forms. The body fluids have to be conserved from excessive evaporation; mechanical support and locomotion have to be adapted for the less dense medium of air; respiration is necessarily performed in a different manner; new food habits have to be acquired; the young have to be carried toward maturity in the egg to insure their survival; or quite different larval stages from those of aquatic forms have to be acquired, as in the insects. This change of environment from the water to the land has been one of the great evolutionary steps of both plants and animals and has resulted in the familiar plants and animals of our own surroundings as well as man himself. In general, the various invertebrate stocks other than the arthropods have become terrestrial in only exceptional cases, such as in the earthworms or the land snails.

The aquatic arthropods were by the very nature of their organization well fitted for terrestrial adventures. Their bodies were encased in a jointed chitinous exoskeleton, practically impervious to evaporation and sufficiently rigid to support them in air. The character of their legs would serve equally for walking on the ground and on the bottom of the ocean; and, as we have already seen, the change from gills like those of a limulus to lungs like those of a scorpion was not profound.

Probably, the arthropods were the first air breathers, but in which group this habit first developed is uncertain. Many students believe that the trilobites gave rise to the terrestrial arthropods. At any rate, this change must have been accomplished early in Paleozoic times, even though it is not until the later Paleozoic that we find any considerable fossil representation of terrestrial arthropods. That the existing Crustacea

are prevailingly marine is no exception to the general argument just outlined as is shown by the land crabs of the tropics, the pill bugs (Isopoda) of our woods and cellars, and the sand hoppers of our shores. The reason that the Crustacea as a whole are aquatic is due to the fact that they represent a line of arthropod evolution which through ages of adaptation has become the scavengers of the sea, while other lines of arthropod evolution have, during the same time, become adapted for terrestrial and aerial conditions of life, so that at the present time the terrestrial and aerial environments are fully occupied by arachnids and especially insects. Hence, there is no sufficient stimulus for Crustacea to forsake their waters, and then, too, the very adaptations which have made them so dominant as aquatic animals have reduced their ability to become adapted to a new environment. In other words, the fact must be recognized that any group of animals which has become specialized in any one direction loses its plasticity to vary in other directions.

As has already been mentioned, the scorpion among the Embolobranchiata is more conservative or primitive in its organization than the spiders and their allies and differs only in certain details from some of the aquatic Merostomata from which it doubtless was derived.

Fossil scorpions have been found in rocks as old as the Upper Silurian—Palæophonus of several species in Europe and Proscorpius in North America. No stigmata (lung openings) have been observed in these earlier fossils and their appendages differ from modern scorpions and are more eurypteroid, so that many students have assumed that they were aquatic in habit, but this is by no means certain. Eoscorpius and other genera from the Carboniferous, however, are like modern scorpions in all essential details.

The spiders and their allies, of which there are a dozen or more orders, depart considerably from the ground plan of arachnid structure as it has been outlined for the Merostomata and the scorpions. Anyone who has watched a garden spider or any other of the numerous kinds all about us will realize that volumes could be written concerning their habits, their nests and snares, and the several thousand existing and several hundred extinct species.

The chief structural modifications have to do with the shortening and loss of contrast between mesosoma and metasoma and

the shortening and more or less loss of segmentation of the whole body. All are relatively small and no giant forms are known in either the past or the present. Most of the recognized orders—indeed, all but one—have been found fossil, but since so much of the geological record comprises prevailingly marine sediments, terrestrial organisms are scarce and sporadic in their occurrence, and spiders are found in abundance only under exceptional conditions, as in the muds of the coal swamps, the Oligocene amber (fossil tree gum), or rather uncommonly preserved lake beds.

There are several classes of arthropods very sparingly or not at all represented in the geological record which were formerly grouped together as the subphylum Myriapoda and represented by the existing centipedes and millipedes. They have a separate head with a pair of antennæ and two or three pairs of mouth appendages, breathe by means of air tubes, and have 12 or more essentially similar and wormlike body segments.

The millipedes (Diplopoda) have 12 to 150 similar segments nearly all with two pairs of short legs, short seven-jointed antennæ, and no compound eyes. Fossils occur in the Devonian, Carboniferous, and Tertiary but are rare and unimportant, as are the relatively few existing forms.

The centipedes (Chilopoda) tend to have flat instead of round bodies and a variable number of segments, each with a single pair of widely extended legs. The antennæ have 14 or more joints. Compound eyes are sometimes present. The extreme of appearance that is more or less typical of the class is seen in the not uncommon centipede of our houses, which is to be considered as a useful rather than harmful animal. It is entirely inoffensive despite its, to some, uncanny appearance and preys on other domestic pests such as silverfish (*Lepisma*) which consume the starch in linens, paper finish, book bindings, and the like as well as on bedbugs, book lice, etc.

The centipedes are closely related to the ancestral insect stock. They occur sparingly as fossils in the Carboniferous and during the Tertiary.

HEXAPODA OR INSECTA (THE INSECTS)

Insects are the most obvious as they are the most abundant arthropods. About half a million species have been described and entomologists have estimated that there are from 2,000,000

to 10,000,000 existing forms. No clime is free from annoying biting or stinging forms, and many transmit the germs of disease such as malaria, yellow fever, African sleeping sickness, and others less malignant; great hosts of other kinds of insects either in their larval or mature stages do incalculable injury to all crops, fruits, or ornamental plants that man cultivates, his carpets and woolens, his furniture and woodwork, and his stored foods of all kinds. Practically every organized government spends vast sums annually in systematized efforts to combat the ravages of insects.

The insects are the most evolved arthropods. This fact is illustrated by their great variety of adaptations; by their remarkable larval stages, unlike anything occurring in other animals; by the manner of life of the so-called "social" insects (ants, bees, etc.); and by their perfection of the art of flying.

Among such a host of forms only the typical ground plan of insect structure can be given. A typical insect has the body divided into three regions—head, thorax, and abdomen. The head has eyes and four pairs of appendages—the antennæ or feelers which are normally sensory in function, and three pairs of jaws comparable with the mandibles and maxillæ of a crustacean. The thorax consists of three more or less consolidated segments each with a pair of legs and the two hinder each with a pair of wings. (Some insects are primitively or secondarily wingless or have the second pair of wings vestigial, as in the flies and mosquitoes.) Abdomen commonly of 10 distinct segments, usually without leglike appendages but carrying at the hind end feelers or stings or ovipositors. Respiration in the adults is by means of air tubes (tracheæ) ramifying through the body, which also give it an advantageous lightness.

Some insects when hatched are essentially like their parents (*e.g.*, cockroaches), although none has developed wings at birth. In the vast majority, the life history may be divided into three stages—larval, pupal, and imagoal or adult—and such insects are said to undergo metamorphosis. The larva may be a caterpillar, grub, or maggot and may be aquatic, subterranean, or a burrower in wood, living on dead organic matter. Larval insects live on solid food, and this stage of the life history may be passed through in a few days or it may last for several years in aquatic forms or subterranean forms. The 17-year locust is, perhaps, the best-known example of the last. At the end of

the larval period the larva usually encases itself in a cocoon of some kind and quietly undergoes a transformation to the mature form. This pupal stage is apt to last through the winter in insects in this latitude. It is dispensed with in aquatic larval forms like those of the dragon and May flies in which the larvæ crawl out of the water, split their skins, unfold and dry out their wings, and fly off.

The striking feature of insect metamorphosis is its origin—a *larval insect is not at all like any ancestor but is an adaptation to* a particular environment and food. Thus, some of our worst agricultural and other pests are the caterpillars of moths and butterflies which as adults are incapable of taking any but liquid food; or in the case of the May fly the aquatic larva may lead a predaceous existence in ponds and streams for several years, existing as an adult only long enough for the female to be fertilized and lay eggs, and then dying without taking any food.

The classification of the insects is in a very unsettled state. *A generation ago, only the following seven orders were recognized*: Hymenoptera (bees, ants, wasps), Coleoptera (beetles), Diptera (flies), Lepidoptera (moths, butterflies), Hemiptera (bugs), Orthoptera (roaches, crickets), Neuroptera (lacewings). Contemporary students recognize from 20 to 44 different orders, which cannot even be mentioned in an introductory account.

No unquestionable traces of fossil insects are known from rocks older than the Carboniferous, but the Carboniferous insects are varied and winged and indicate a long antecedent (if unknown) evolution.

The most commonly preserved insects in the Carboniferous are the cockroaches, of which several hundred species have been described. They are readily recognized by the characteristic arrangement of the wing veins and are more like modern roaches than are any of their contemporaries. Another interesting group represents the precursors of the dragon flies, one of which—Meganeura of the French Coal Measures—had a wing expanse of about 30 inches and is the largest known insect.

The most primitive of the Carboniferous insects is the order Palæodictyoptera—a group which is supposed to have given rise to most of the extinct Paleozoic orders which, in turn, gave rise to the modern orders.

The Palæodictyoptera had two pairs of equal wings with a very primitive type of veining. Over 100 species in a considerable

number of families have been discovered, and among these the genus Stenodictya (Fig. 111), if the fossil remains have been correctly interpreted, is the most remarkable. The head was moderately large and rounded, with simple antennæ and mouth parts suitable for biting. The three segments of the thorax are distinct and each is provided with a similar pair of legs; the first segment has a rigid winglike projection at each side; and the second and third segments have similar nearly equal wings capable of only an up-and-down motion. The abdomen consisted of 10 similar segments and was terminated by a pair of feelers (cerci). Each abdominal segment had a small chitinous

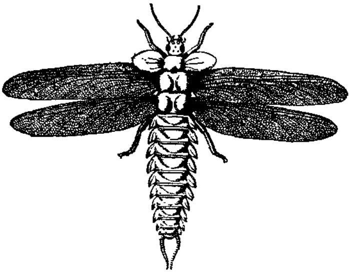


FIG. 111.—A primitive insect, Stenodictya. (*After Schuchert.*)

winglike projection on each side, like those of the first thoracic segments but smaller. These are believed to have been aids and guides in flight like the wings of an airplane and to hint at the manner in which the true wings originated.

Very few insects have been discovered in the Triassic, but they are fairly plentiful in the Jurassic. Cretaceous rocks, which are so largely of marine origin, have furnished relatively few insects, but large numbers have been described from the Tertiary. Except under exceptional circumstances, such as the wonderful insect assemblage found in amber or other fossil gums, the insect fossils tend to be crushed or otherwise distorted and confused and the majority of the fossils represent wings only. Consequently, much study has been given to wing venation and several elaborate systems of names have been devised for the various veins.

The known Mesozoic and later insects are essentially modern in appearance and affinities.

Although the precursors of the modern orders in the late Paleozoic are encountered, these late Paleozoic dragon flies, May flies, etc., are, for the most part, sufficiently different to be referred to distinct and extinct orders. The first true alder flies appear in the Triassic. In the Jurassic the following types make their appearance in the fossiliferous record: locusts, crickets, mantis, beetles, the more primitive Hymenoptera (the true ants, bees, and wasps are not certainly found until later), true dragon flies, scorpion flies, caddis flies, butterflies, moths, true flies, and primitive plant lice. The Eocene introduces termites, grass-hoppers, and earwigs. In the Oligocene are the oldest known stick insects, book lice, and fleas.

CHAPTER XI

VERTEBRATA

With rare exceptions the fossil remains of vertebrates consist of bones and teeth, or dermal hard parts such as the spines and scales of fishes, or, more rarely, feathers of birds. Fishes and small amphibians are sometimes preserved as impressions, and occasionally a mummy will be more or less preserved under exceptional conditions of sedimentary burial, as in the remarkable dinosaur occurrences of the Cretaceous or the frozen elephants of the Pleistocene, but for any adequate knowledge of the paleontologic history of vertebrates it is the bones and teeth upon which we are forced to rely. The fossil hard parts of the vertebrates, especially as we ascend the scale of organization, are much more reliable in their indications of the structure of the soft parts and the habits of their owners than are the hard parts of invertebrate animals, since the vertebrate is a so much more complex organism and the skeleton is an internal mechanism rather than a protective external crust.

CHORDATA

Man is a land animal, his familiar associates are the domesticated animals which supply him with food, the dogs and cats, and the birds of the orchards and hedgerows. Most of the invertebrate phyla are marine, and those that are not, such as the insects and spiders, are generally thought of as pests rather than as fellow animals, so that the term "animal" to most probably means a vertebrate. Since self-interest has demanded that man know his own structure and functions and those of the animals but little lower in the scale whose structure and functions are so like his own, a more detailed knowledge exists of the vertebrate animals than of any other phylum.

The ground plan of vertebrate structure is easily understood. The framework or skeleton which supports the soft parts is within, not on the outside, as in most invertebrates. It comprises an axial skeleton with the skull at the front end and, articulating

with the base of the skull, a vertebral column extending backward into the tail and consisting of articulating vertebra some of which may support ribs. There have never been more than two pairs of limbs, and the limb skeleton consists of a variety of articulating bones, the proximal limb bones articulating onto a more or less rigid support or limb girdle—a shoulder or pectoral girdle for the forelimbs and a pelvic girdle for the hind limbs. As regards the fleshy clothing of this skeleton it comprises the nervous, respiratory, circulatory, muscular, generative, and alimentary systems. Most important of these as regards the general ground plan of the vertebrates are the central nervous system running along the dorsal side of the vertebral column and enlarging at its front end to form the brain; the alimentary canal with the associated organs of respiration; the main trunks of the circulatory system; and the reproductive organs occupying the larger or ventral side of the vertebral column—opposite to the normal relations in the invertebrates.

The most primitive vertebrates are the fishes, and the simplest of these without bones and with an unossified axis—the notochord—clearly point backward to the line of ascending evolution through the primitive Chordata represented in existing seas by the free-swimming larval ascidians or tunicates (the adults are specialized for their floating or sessile mode of life and have lost most traces of this relationship) and by such worm relatives as Balanoglossus. Of course, neither the Balanoglossus nor the tunicates nor the lancelet are true missing links and biologists are woefully ignorant of the time, place, and manner in which the stages from invertebrate to vertebrate were passed through, but they are not far wrong in looking to the worms as the most promising ancestral group, although there are some who hold other views.

Undoubtedly, also, the early seas must have had their fauna of Chordata some of which were the ancestors of the existing ascidians and lancelets and others the beginnings of the line which finally culminated in true vertebrates. These were all small, entirely soft-bodied forms entirely incapable of being preserved in the rocks, so that what they were like can be only vaguely inferred from the knowledge of existing forms and the hard parts of such of the early vertebrates as have been found fossil.

We need not concern ourselves with the various attempts of zoologists to frame a satisfactory classification of the Chordata,

for, in paleontology, we have only the familiar groups of fishes, amphibians, reptiles, birds, and mammals with which to deal, no representatives of the classes Urochorda (ascidians), Hemichorda (Balanoglossus) and Cephalochorda, or Euchorda Acraniata, (lancelets) have been, nor are they likely to be, found fossil, since they are entirely soft bodied.

THE FISHES

It will be simpler to consider the fishes as a single class Pisces (from the Latin *piscis*, a fish) of the vertebrate phylum, although sometimes they are grouped in the four classes—Cyclostomata, Arthrodira, Ostracoderma, and Pisces. The most recent work has shown that the existing Cyclostomata and the Paleozoic Ostracoderma are closely related to one another, and there are indications that the Arthrodira may be related to the shark stock (Elasmobranchii or Selachia).

Fishes may be defined as cold-blooded aquatic animals, usually breathing exclusively by means of gills but supplementing this method in some of the more primitive groups (lobe fins and lungfishes) by atmospheric air taken into the swim bladder. Limbs in the form of fins. Skin moist and slimy, rarely naked, usually covered with scales or bony plates. Vertebral axis ending in a vertical tail fin. Heart with a single auricle and a single ventricle. Reproduction by means of eggs, which are numerous and small. Embryo without amnion or allantois.

The dermal or skin structures are scales, plates, spines, fin rays, and teeth.

Scales.—The character of the scales in the fishes is of considerable value in indicating relationships. Louis Agassiz recognized four kinds of scales which corresponded with the four orders of fishes which he recognized. These were placoid, ganoid, cycloid, and ctenoid scales.

Placoid Scales.—These characterize the sharks and rays and are rhombic to conical, constructed much like teeth, with a bony base penetrated by blood vessels and covered with dentine and an outer layer of enamel. They lie close together in the skin like a mosaic and may be of considerable size or tiny and are often of different size and form on different parts of the body.

Ganoid scales are generally larger than placoid. They are rhombic or rounded in outline—the rounded usually overlapping like shingles or tiles on a roof, the rhombic usually articulating

by an underlapping toothlike process, each one fitting into a hollow on the inner side of the next. They consist of a bony basal plate covered with a layer of enamel which is usually thick and shining. Such scales characterize the so-called "ganoid" fishes, the lobe fins, some of the lungfishes, and modern garpikes.

Cycloid scales are thin, elastic, rounded or elliptical polygonal shapes of a transparent, shiny, phosphatic surface layer and a base of connective tissue and generally overlap like shingles

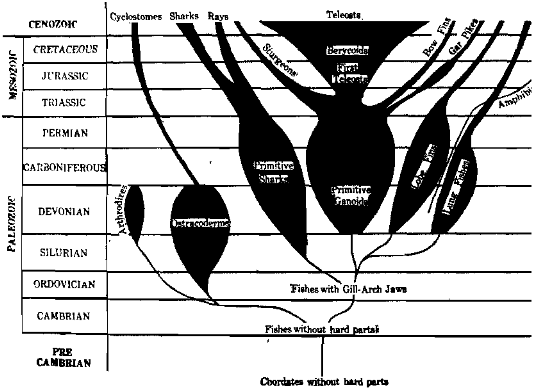


FIG. 112.—*Relationships, relative abundance, and geologic history of the fishes. (After Gregory.)*

on a roof. The surface is usually marked with concentric and radial lines. They characterize the vast majority of living fishes and grade into the ctenoid scale which is like a cycloid scale except that its hinder part has a series of parallel ridges which look like the teeth of a fine comb and which may project as points along the border.

Spines.—Spines because of their imperishable nature are frequently found fossil, although their owners long since rotted away. They may be of bony tissue or have an enamelled outer surface like ganoid scales. They occur on the head or in connection with the fins, often assuming characteristic shapes and

attaining considerable size. They are to be regarded as skin structures akin to the normal rays which strengthen the fins. The fins are folds of skin supported, to varying degrees, by parts of the internal skeleton and by dermal rays.

Vertebral Column.—Starting as a notochord inherited from the simpler Chordata, this becomes encased in ringlike segments of partly or completely cartilaginous or bony substance. In those fishes which have a bony axis the individual vertebræ are *biconcave, allowing great flexibility.*

Skull.—The skull of fishes is much more complex than it is in the higher vertebrates. It may be entirely of cartilage, as in the sharks, or a greater or lesser number of bony elements may enter into its construction. Its details are too elaborate for consideration here.

Form of Fishes.—The normal shape of a fish is that of a compressed spindle, mechanically adapted to slip through the water with the least friction. The front end is bluntly conical and is the most rigid part; the hinder portion tapers and is pliable. Swimming is accomplished chiefly by the rapid sculling motion of the vertical tail fin. The lateral fins lie flat against the body when swimming and are used for slowing or turning. This typical fish form, often called the "stream-line form," is approximated by all swiftly swimming animals such as certain squids, aquatic mammals like whales or dolphins, and aquatic reptiles like ichthyosaurs. It is undoubtedly an adaptation to speed in aquatic animals and shows clearly that the fishes originated in the seas, although some theorists have claimed that the typical fish form was brought about by the influence *of flowing water and that, therefore, the fishes originated in* rivers, which is putting the cart before the horse, for in all animals that have assumed this form it is the animals that move and not the medium.

Of course, many fishes have departed from this typical form in response to other habits of life. Thus, among the earliest known fossil fishes, the body is depressed and armored and they were sluggish bottom dwellers. Among modern forms with somewhat similar flat bodies and sluggish habits are the anglers, flounders, soles, skates, and rays. Many others have high compressed bodies like sunfishes and are slow swimmers, spending most of their time basking. Others are narrow shaped like the pike or the pickerel and are darters in habit, lying in wait and

swooping upon their prey. Others are elongated and wriggle through the water like eels, and others are intermediate between these main types. Time and again during their history these adaptations have appeared in different lines of descent in response to the corresponding habits of life (Fig. 113).

The ancestral boneless fishes had as their most outstanding feature an axial notochord or elastic rod extending practically

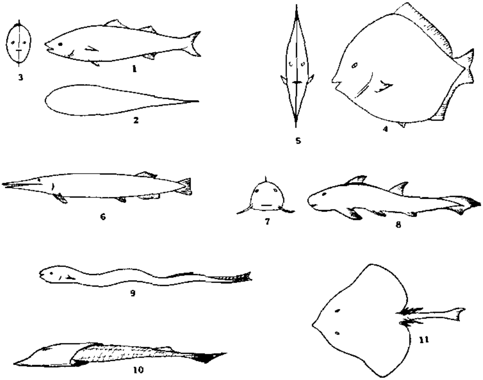
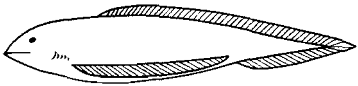


FIG. 113.—Principal modifications of the body form in the fishes. 1, 2, 3. The compressed fusiform speedy form in side, top, and front view. 4, 5. Narrow, high, slow form in side and end view. 6. Arrow-shaped darting form. 7, 8. Elongate fusiform intermediate between 1 and 9. 9. Elongate eelike, swift or slow and mostly bottom dwellers. 10, 11. Depressed and slow bottom dwellers.

the whole length of the body immediately below the hollow nerve trunk. As the evolution of a skeleton proceeded, rings of cartilage were formed around the notochord and these eventually became hardened by the deposition of lime salts. From these cartilage rings, which are the future centra of the vertebræ, paired extensions arched upward around the nerve trunk or spinal column which thus becomes encased in bone. At the forward end, these processes grew around the forward end of the spinal column to form a case or cranium for the evolving brain. Opposite the developing brain case, other cartilaginous

and eventually bony processes grew downward between the gill openings. These are the gill arches, and it is the elaborated *and modified first gill arch which eventually gave rise to the* jaws. We still have a group of living fishes—the Cyclostomata or lamprey tribe—which lack jaws, and this was also the case in the Paleozoic ostracoderms. The balance of the known vertebrates have jaws and are often known as the Gnathostomata in allusion to this fact and in contrast with the Agnatha or jawless types.

The ossification of the vertebra and brain case and the formation of gill arches and jaws were most important events in *vertebrate evolution without which the development of the later* and more specialized types would have been impossible.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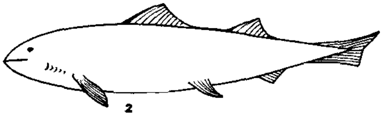
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FIG. 114.—Showing the primitive fin folds (1) and the modern fins (2).

Along with the evolution of the axial skeleton just described, the surface of the primitive fish was thrown into skin folds as an aid to swimming heretofore accomplished by an eellike motion. One *such fold of skin extended along the middle of the back* around the tail and forward part way along the underside nearly to the anus. From this point forward to the region of the gills it was replaced by a pair of horizontal folds one on either side of the lower part of the body. These skin folds or fin folds were originally continuous but eventually they enlarged at the points of mechanical effectiveness and diminished in the intervening region, becoming reinforced where used by stiffening material—at first of cartilage and subsequently of bone, derived, in part, *from the skin and, in part, from the internal skeleton.* Such was the origin of the fins with their spines or rays. From these simple beginnings there resulted the limbs, which were destined

to play a part so important in the evolution of the terrestrial vertebrates.

The tail fin in fishes was primitively almost separated into nearly equal upper and lower parts or lobes by the hind end of the body. Such a fin is called "diphycercal" (Fig. 115[1]). This became modified by a slight upward curving or tilting of the end of the body resulting in the gradual reduction of the upper lobe and an expansion of the lower lobe. This condition is known as "heterocercal" (Fig. 115[2]). These two with various intermediate stages are common among Paleozoic fishes but have been largely replaced since the early Mesozoic by a tail fin known as "homocercal," in which the pointed end of the body becomes rounded off, and a nearly symmetrical two-lobed fin represents the original ventral lobe of the diphycercal condition the dorsal lobe of which is almost or completely supressed (Fig. 115[3]). These names are compounded ot the suffix *cercal* from the Greek word for "tail," *diphy* ("two kinds"), *hetero* ("unlike" or "unsymmetrical"), and *homo* ("alike" or "symmetrical").

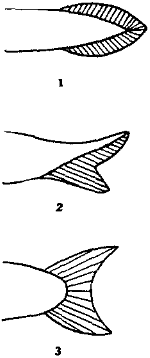

FIG. 115.—Showing the three principal types of tail fins. 1. Diphycercal. 2. Heterocercal. 3. Homocercal.

Fishes are almost inconceivably ancient and for many millions of years they were the sole representatives of the vertebrate phylum. The most ancient that are found fossil belong to the group known as "ostracoderms" or "bony-skinned fishes," so named because their skeleton was in the form of an external armor and their internal skeleton remained unossified. They appeared in the Ordovician, reached their maximum during the Silurian, and gradually became extinct during the Devonian. The head and the front part of the trunk were enclosed in an external bony case made up of several fused pieces, with a pair of eye openings and a median nostril opening on the upper side and a large mouth opening on the ventral side. The mouth was without hard parts. Paired fins were apparently absent except in one of the four orders into which they have been divided (Antiarcha) in which there is present a pair of armored pectoral

appendages. *Although some ostracoderms are shaped like* free-swimming fishes (Birkenia), the majority are broad and flat.

It is doubtful if nature's first attempt to evolve a fish is fairly represented by the ostracoderms. The first fishes would lack hard parts and *fail of preservation*, and the wonderful array of ostracoderms in the older Paleozoic represents an early adaptation to a mostly sluggish and bottom-dwelling existence, swift unarmored types being always antecedent to slow armored types.

The Arthrodira comprise a group of extinct fishes of late Silurian and Devonian times of uncertain relationships which have sometimes been grouped with the ostracoderms and sometimes considered to be related to the lungfishes or sharks. The head and trunk were armored with bony plates jointed at the neck; the bony jaws were powerful dermal ossifications and not articulated with the skull. The internal skeleton was partially ossified; but the central axis remains a wholly or partially uncalcified notochord. Coccosteus is, perhaps, the best-known genus. In the Upper Devonian, Dinichthys reached a hugh size, with a head about a yard long and nearly as wide. Members of this genus are a relatively short side line, off the main lines of fish evolution.

The primitive sharks which appear in the geological record during the Silurian are not far from the main line of evolution leading to the more modern types of fishes. The sharks largely retain a skeleton of cartilage partially calcified but not ossified to form a complete bony skeleton and have their skins covered with placoid scales. They are of normal shape with a somewhat flattened head and protuberant snout, the mouth generally on the underside of the head, and a long, slender tail, usually heterocercal. The five gill slits on either side of the neck are exposed or covered with a flap of skin and never with a bony cover. The median fins are often provided with horny or bony spines and it is these spines and the teeth which are commonly preserved as fossils.

The relations of the jaws to the cranium, the character of the notochordal axis, and the manner and degree of its calcification are often used as classificatory features. Among the diversified adaptations seen in Paleozoic sharks the oldest known (Acanthodian) shows the nearest approach to the theoretical horizontal pair of fin folds which are supposed to have given rise to the paired fins of fishes (pectoral and pelvic fins) (Fig. 116[1]). In

such a genus as Climatius of late Silurian and early Devonian times, a row of spines extended from the pectoral to the pelvic fin on each side and each formed the front border of a fin membrane.

In Mesacanthus of the Lower Devonian the pectoral and pelvic fins are enlarged and the intermediate ones are reduced in size

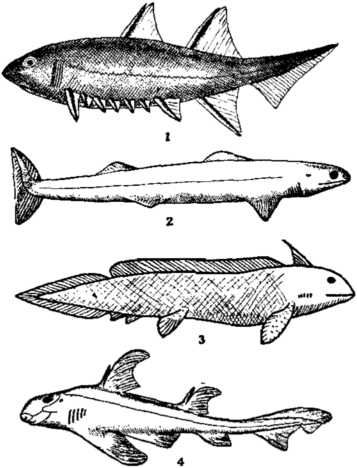

FIG. 116.—Showing various types of sharks. (*After Schuchert.*) 1. The Lower Devonian acanthodian Climatius. 2. The Upper Devonian cladoselachian Cladoselache. 3. The Upper Carboniferous pleuracanthidian Pleuracanthus. 4. The living Port Jackson shark. (All much reduced.)

and number. In Acanthodes of the later Paleozoic the intermediate spines and fins had disappeared. The acanthodian sharks were small, rarely over a foot in length. The second Paleozoic shark type is known as Cladoselachian, from the best-known genus Cladoselache of the upper Devonian (Fig. 116²). The body form is elongated and round bodied with a strongly heterocercal tail. The paired fins are supported by unjointed

parallel rods of cartilage, partly fused at the base and extending radially to the edge of the fin and once thought to be the prototype of the terrestrial vertebrate limb. The third Paleozoic shark type, known as the Pleuracanthidian, is especially characteristic of the later Paleozoic (Carboniferous and Permian) and ranges into the earlier Mesozoic (Fig. 116[3]). The earlier forms do not differ greatly from Cladoselache, but the later forms evolve into slower, elongate, more or less eel-shaped forms with diphycercal tails.

Sharks were very abundant in the Lower Carboniferous, less common in the latest Paleozoic, the modern types appearing in the early Mesozoic and increasing in abundance down to the present.

The cladoselachian sharks of the Paleozoic, as well as the Mesozoic and later sharks, were largely active, predaceous types, although, as we have seen, elongate, sinuous forms had evolved in the Carboniferous (pleurocanthidian) and somewhat similar forms, like the frilled shark (Chlamydoselache), occur in existing seas. *A depressed body form indicating slower bottom-dwelling* types is already approximated by the cochliodont sharks of the Carboniferous and Permian and reaches its extreme adaptional development in the angel fishes, rays, and skates of Jurassic to Recent times.

The great naturalist Agassiz proposed the subclass Ganoidei for those fishes, abundant in the Devonian and still existing in limited numbers, which had the body covered with the type of scale called "ganoid," that is, consisting of an inner layer of bone and an outer layer of enamel. At least four orders were recognized, one of which was the lobe fin or Crossopterygii, and the Latin name and old conception of the group is less and less used by students of fishes. The popular term ganoid, however, is likely to survive as the collective designation for that progressive fish stock derived from sharklike ancestors, which, clad in their coats of mail of enameled scales, dominated the waters from Devonian to Middle Mesozoic times, giving rise to a variety of adaptations at different times and gradually merging into the true bony fishes—the latter the dominant fishes of the world since Cretaceous times—the ganoids surviving in limited numbers in modern times as the scaleless paddle fish; the mud grubbing sturgeons in which the body is partially covered with large bony plates; the gar pikes of southern North America—

this "die hard" of the ancient line still wearing his armor as in the olden days—and the bowfins of the southern United States—a sluggish fresh-water fish in which the scales have become thin and overlapping like cycloid scales but still show microscopic traces of the inner bony layer that reveals their ancestry.

DIPNOI OR DIPNEUSTI (LUNGFISHES)

The early fish stock which gave rise to the primitive sharks also gave rise to a more progressive group collectively called the "ganoid stock," which evolved along various lines, early diverging to form the groups known as the "lobe fins" (Crossopterygii) and the "lungfishes" (Dipnoi). The ganoids survived down to present times in the relatively few gar pikes, bowfins, and sturgeons. This same ganoid stock in the early Mesozoic gave rise to the true bony fishes (Teleostei) which have so largely replaced the earlier ganoid evolutionary lines in modern waters.

From the point of view of general vertebrate evolution, the lobe fins and the lungfishes are the most interesting of fishes, since they furnish objective illustrations of the way in which terrestrial limbs and air-breathing lungs originated.

The lungfishes are characterized structurally by an only partially ossified skeleton, with many membrane bones. The internal skeleton is chiefly cartilaginous but the vertebræ, arches, ribs, and fin supports all tend to be more or less ossified. The air bladder or swim bladder is modified to form a single or double elongated sac with cellular spaces over which the blood vessels ramify and return the oxygenated blood to the heart. This air bladder is connected by a short tube with the front wall of the gullet and serves as a lung supplementing the respiration of the gills (hence, the name from the Greek words meaning "double breathing"). Paired fins with a segmented cartilaginous axis. Tail diphycercal or heterocercal. Lower jaws articulated only with upper—that is, the hyomandibular portion of the first gill arch has no share in the jaw articulations, a condition known as "autostylic," which distinguishes the lungfishes from all other ganoids and teleosts. Nostrils open into mouth, the usual method in higher vertebrates, but rarely found among fishes.

The lungfishes appear in the Lower Devonian, the earlier forms being similar in form to the contemporaneous ganoids. They

show considerable diversity of form and after the Devonian commence to elongate, the heterocercal tail tends toward diphycercal and they evidently were already becoming modified toward

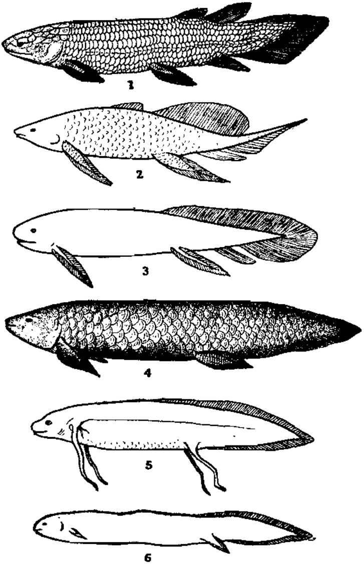

FIG. 117.—Fossil and existing lungfishes. 1. The Lower Devonian Dipterus. (*After Woodward.*) 2. The Upper Devonian Scaumenacia. (*After Hussakof.*) 3. The Upper Devonian Phaneropleura. (*After Page.*) 4. The Australian Neoceratodus. (*After Schuchert.*) 5. The African Protopterus. (*After Miall.*) 6. The South American Lepidosiren. (All much reduced.)

those habits which characterize the still existing species. During the Mesozoic the genus Ceratodus attained a world-wide distribution. Today, the three peculiar genera Protopterus, Lepidosiren, and Neoceratodus are all that are left. Their limited distribution and peculiar habits make them exceedingly

interesting, but in no sense are they missing links between the fishes and amphibians. They merely furnish illustrations and hints of how a fin could become modified into a leg and a swim bladder into a lung, as is undoubtedly what took place in giving rise to the amphibians in the Silurian or Devonian.

The Australian lungfish (Neoceratodus) is found in pools and water holes in a limited area in Queensland. Its air bladder is *double like the lungs of terrestrial vertebrates. It is a large,* wormlike, inactive, sluggish fish. It habitually rises to the surface and gulps air to supplement the gill respiration, especially during the summer season when the water becomes foul, being able to survive conditions under which the associated fishes die in large numbers. It is not known to hibernate like the African and South American forms, nor can it leave the water or support its bulk on its relatively feeble fins.

The *African lungfish* (Protopterus) has a single air bladder. It is rather widely distributed from the Senegal and White Nile to the Congo and Zambesi rivers. Three species are known. They are carnivorous and haunt the river marshes. They are more active than the Australian lungfish and the fins are long and frequently used like incipient legs for supporting the body on the bottom or for crawling. When the dry season comes on, they burrow a foot or two in the mud and encase themselves in a capsule of hardened slime and mud, hibernating until the next rains, breathing solely by means of the air bladder. The young have external gills like those of a salamander, which are reduced when they are about 2 months old and the air bladder has commenced to function.

The *South American lungfish, often called the "mud fish"* (Lepidosiren), has a single species in the Amazon and Upper Paraguay, chiefly in the overflowed marshlands. It is the most wormlike of all in appearance. At the approach of the dry season it hibernates in burrows much as does Protopterus, which it also resembles in its development.

The lobe fins or fringed-finned ganoids (Crossopterygii) are a group contemporaneous with the earliest lungfishes and, like *them, an early modification of the primitive ganoid stock. They* get their name from the fact that the paired fins have an internal bony axis covered with skin and scales and fringed on both sides by dermal rays, thus constituting a much more likely prototype of the limbs of terrestrial vertebrates than the fins of the lung-

fishes. The notochord may be persistent, or the vertebræ may be ossified; an infraclavicle is present in the shoulder girdle.

Like the lungfishes, the existing lobe fins take air in the swim bladder for purposes of respiration but the air bladder is not so lunglike as in the existing lungfishes. Our interest centers in

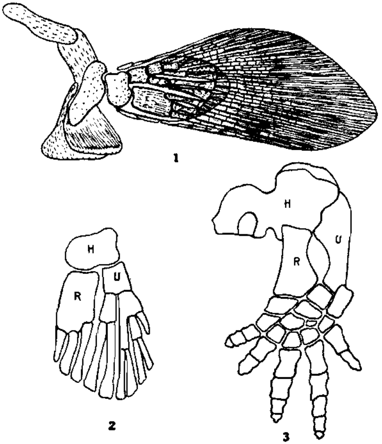

FIG. 118.—Showing the origin of the terrestrial limb in vertebrates. (*After Gregory.*) 1. Right shoulder girdle and pectoral fin of the Upper Devonian Sauripterus. The inner curved line shows the outline of the fleshy, scale-covered part of the fin which encloses the prototype of the humerus, radius and ulna, carpals, and digits—parts of the internal skeleton—and the fringed rays along the edge which were of dermal origin. 2. The internal bony part of the preceding fin without the shoulder girdle or dermal rays, for comparison with. 3. The right limb of Eryops, a large North American terrestrial amphibian from the Permian belonging to the order Stegocephalia. H. humerus; R. radius; U. ulna.

the limblike character of the paired fins, sufficiently explained in the diagram (Fig. 118). The lobe fins make their appearance in the geological record in the Devonian—the Lower Devonian genus Osteolepis being probably the best-known fossil type. They wane after the Paleozoic and exist in two African river fishes—Polypterus and Calamoichthys—the latter an eel-like

form. Polypterus often supports its body above the bottom by means of its pectoral fins and the length of these fins in such Upper Devonian genera as Holoptychius and Sauripterus indicates a like habit; most vertebrate paleontologists believe that the limbs of land vertebrates were derived by modification of this type of fin.

TELEOSTEI (BONY FISHES)

One of the most obvious distinctions between the ganoids and the true bony fishes (*teleostei* means "true bone") consists in the replacement of ganoid scales by thin, elastic, overlapping cycloid (or ctenoid) scales. There are various anatomical characters that separate the two which it is usually impossible to verify in fossils so that no clear line of demarcation can be drawn, and during the Jurassic the bony fishes appear to emerge gradually from the ganoids. By Cretaceous times bony fishes become common, and during the Cenozoic they largely crowd the older types into the nooks and corners of the fish world. They are today extraordinarily varied and numerous and have become adapted to the wide range of environments found in seas, rivers, and lakes, including even the perpetually dark and cold depths of the ocean basins. Some are conservative in their structural features, and others progressive. A modern perch might be considered an average type. They assume all of the earlier body forms. Nearly all the food and game fishes are true bony fishes.

Among their more marked features are the spiny (actinopterygian) fins, simplified jaws, and relatively larger head; the tail in both its outer form and internal structure is homocercal. Frequently, the pelvic girdle moves forward from near the transition region between the trunk and the tail and becomes attached to the shoulder or pectoral girdle so that the ventral fins are below and only slightly behind the pectorals. The gills are covered by an operculum and the air bladder when present is a hydrostatic organ and not a lung, losing its connection with the œsophagus. Numerous intermuscular bones are often developed, as in the shad.

CLASS AMPHIBIA

Those fishy pioneers with air bladders like those of the lungfishes and paired fins like those of the lobe-finned ganoids, which,

after ages of using their fins for pushing and paddling themselves over mud flats, gradually ventured onto drier and drier ground, where they had no competition for air and where they avoided the competition for food in an almost wholly aquatic organic world and the dangers of the swarming hordes of ganoid pirates of the waters, were the ancestors of the amphibians. These pioneers on the land laid the foundation for that long line of four-limbed terrestrial vertebrates which ultimately conquered both the earth and the air and eventually culminated in man.

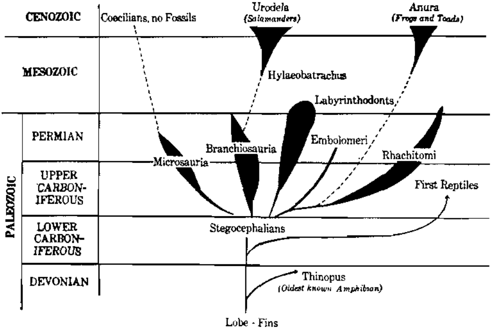

FIG. 119.—Diagram showing the relationships, relative abundance, and known geologic history of the Amphibia. (*After Gregory.*)

Of course, this forsaking of the waters for the land was a slow and entirely unconscious adaptation and probably no single factor can be considered to offer a satisfactory explanation. Possibly, natural selection, weeding out the unfit in fresh waters which were more or less seasonal in character, was the most important factor in bringing about the adaptation to a wholly new environment. The time when this event took place is uncertain but it may well have been in late Silurian, for a good-sized amphibian footprint—the oldest known trace of this class of vertebrates—has been found in the Upper Devonian of Pennsylvania and christened *Thinopus antiquus*. Footprints and bones of amphibians are not uncommon in the Carboniferous, and before the close of the Paleozoic the Amphibia had become

world wide and varied and had probably given rise to the Reptilia.

Their relationships, relative abundance, and known geological range are shown in the diagram (Fig. 119).

The Amphibia get their name from the Greek words *amphi* meaning "both" and *bios* meaning "life," in allusion to the fact that the eggs hatch in water and the young are aquatic like the tadpoles of a frog or toad, breathing by means of gills, some becoming transformed at maturity into four-limbed air breathers—hence, leading a double life. Others remain aquatic through life.

Amphibia have moist and slimy skins like their fish ancestors. They lay numerous small eggs which are in no way protected from drying and must, therefore, be laid in water or in moist places. Since the eggs are small, they contain a limited food supply for the embryo, which thus hatches in a short time and as a larva with plumose gills, which must continue through adolescence in the water while its lungs, legs, and other terrestrial features are being evolved. Hence, it can be said, that the necessity of water to protect the eggs of an amphibian chained this class to the vicinity of water and made them spend part of their lives as aquatic gill breathers.

In appearance the amphibians resemble reptiles more than they do fishes, but structurally they are more like their fish ancestors; in fact, many naturalists divide the vertebrates into three major groups—the Ichthyopsida, to include the fishes and amphibians; the Sauropsida, to include the reptiles and birds; and the Mammalia. The Amphibia differ from fishes in never having fin rays, in usually lacking skeletal elements in the skin, and in having the same limb bones as the higher vertebrates. They are cold blooded with a three-chambered heart, no diaphragm, two occipital condyles, no sternal ribs, and many other distinctive anatomical features.

They are divided into four orders of which three are existing and three are found fossil. The existing orders are the Gymnophiona or cœcilians, which are simplified, warm-climate, snake-like forms in which the limbs have been lost, and which are unknown as fossils; the Urodela or salamanders which live in aquatic or moist environments and may retain their gills through life; and the Anura or frogs and toads, which are usually without tails at maturity and have the hind legs longer than the front ones. Both the Urodela and Anura are rare as fossils except

in very late deposits. They both appear in the geological record in Middle Mesozoic times, and their supposed relationship to ancestral extinct forms is shown in the geneological diagram. The fourth order—the Stegocephalia—has been wholly extinct since the Triassic. Its represents the original stock of both the later Amphibia and the later Reptilia and is of great interest to the paleontologist and the student of evolution.

The Stegocephalia (solid headed) are so called because the cranium had a continuous bony covering and the only openings in it were for the nostrils, the eyes, and, behind the eyes, a central opening for the so-called "pineal eye." The teeth were conical and sharp, not set in sockets, and sometimes complicated in structure by the enfolding of their dentine and enamel coat.

The Stegocephalia range through the later Paleozoic and Triassic and contain the largest known amphibians. They are salamander or lizard-like in appearance, always with a tail, and, in most cases, two normal pair of limbs. Unlike recent amphibians, they possessed more or less of an external armor of bony plates developed chiefly on the underside of the body. The vertebral column is primitive in that the notochord persists as in the ganoid fishes, and in only the most specialized Stegocephalia is it completely interrupted by the ossification of the centra of the vertebræ.

The degree of specialization of the vertebral column is one of the important features for distinguishing the different lines of evolution. This was contemporaneous with their geographical spreading, which probably began in mid-Devonian and they found ideal environments in the extensive coal swamps of Carboniferous times. During the Carboniferous and Permian they show a variety of body form due to their differing habits and habitats—slender and active aquatic swimmers with sharp teeth, such as was Cricotus of the Texas Permian. Eel-like bottom dwellers like Ptonius (Fig. 120[3]) of the Carboniferous with dwindling limbs, swimming as a snake swims. Large, wide, flat-headed sluggish bottom dwellers like the Permian Diplocaulus. Long-headed, slow-moving, alligator-like forms such as Archegosaurus of the Permian, which reached a length of 5 feet. The truly terrestrial were long and massive-headed, short-bodied, and short-tailed, stout-limbed forms like Cacops (Fig. 120[4]) or Eryops, the latter four times the size of Cacops of the Permian.

The Branchisauria (Phyllospondyli) were small, 4 to 8 inches long, with flat, semicircular-shaped heads, simple, hollow teeth, short, straight, single-headed ribs, and thin scales. The notochord persisted throughout life, becoming only slightly constricted by the hollow cylindrical vertebræ, each of which consisted of a right- and left-hand piece. They ranged pretty well through the Upper Carboniferous and Permian and in places are exceedingly abundant in lower Permian rocks. They greatly resembled a modern tadpole in appearance (Fig. 120[1]).

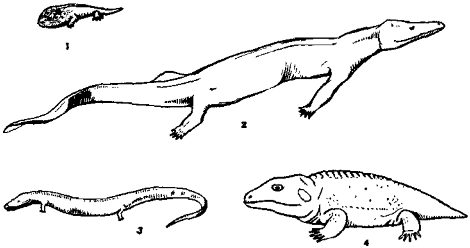

FIG. 120.—Showing adaptations in Paleozoic amphibians. (*After Williston.*) 1. The tadpole-like Branchiosaurus from the Permian of Saxony. 2. Cricotus, a large, newtlike swimming form from the Permian of Texas. 3. Ptyonius, an eellike adaptation from the Carboniferous of Ohio. 4. Cacops, a terrestrial form from the Permian of Texas. Eryops, a similar form from the same region, was four times as large as Cacops. All are drawn to scale and are about one-tenth life size.

The Microsauria (Leptospondyli), with a somewhat shorter racial history, were long tailed and salamander-like. They had long, slender, generally double-headed ribs, and the persistent notochord was constricted by the encasing, hourglass-shaped bony vertebræ.

The Temnospondyli, which comprises the groups known as Rhachitomi and Embolomeri, usually had the base of the skull (basioccipital) completely ossified, which was not the case in the preceding groups, and had their vertebræ made up of several independently ossified bones. In the Rhachitomi the vertebral centra consist of a horseshoe-shaped basal piece (hypocentrum) and a pair of lateral pieces (pleurocentra) as well as the neural arch and its processes above. In the Embolomeri the pleuro-

centra unite with the hypocentrum to form a complete bony ring which unites with the neural arch above.

The Labyrinthodontia (Stereospondyli) are so called because the enamel of the teeth becomes infolded in the dentine in a complicated way so that in a cross-section of a tooth the pattern is labyrinthine in appearance. The labyrinthodonts were especially characteristic of the Triassic and some attained a length of 8 or 9 feet. They were heavy, clumsy animals with large heads, bulky bodies, and short tails. The base of the skull, as well as the wrist (carpus) and ankle (tarsus) bones, were always ossified. *The centra of the vertebræ were solid bony disks.* All of the stegocephalians made footprints and many of these were preserved as fossils, such as those in the Permian of the Grand Canyon or some of those for which the Triassic is noted both in American and in Europe.

REPTILIA

Under the Amphibia it was pointed out that their development confined them to a rather limited and prevailingly moist environment. The great step toward a completely terrestrial adaptation was taken by the Reptilia. This consisted in laying larger eggs with abundant yolks so that a sufficient food supply enabled a postponement of hatching until the embryo had developed to a point where it closely resembled its parents. More important still, their eggs were covered by an impervious protective shell and, therefore, could be laid upon land instead of in water.

Along with this the Reptilia lost the moisture glands of the skin which kept the Amphibia moist and slimy and, thus equipped to resist evaporation both as adults and embryos, rapidly replaced the Amphibia as the dominant land animals, and were able to cultivate all sorts of terrestrial environments during their wonderful adaptive radiation over the earth in the closing days of the Paleozoic and in the succeeding Mesozoic, so that the Mesozoic era is often called the "age of reptiles." Many became readapted to a wholly aquatic existence, while others developed the power of flight, so that in the late Mesozoic heyday of their reign, the reptiles dominated on land, in the air, and in the sea. Their relationships, relative abundance, and geologic history are shown in the diagram (Fig. 121).

The living reptiles comprise the groups to which the turtles, crocodiles and alligators, lizards and snakes belong, and although

these live in a greater variety of habitats and have a great variety of habits, they give but little indication of the wonderful evolution of the reptiles during geological time, especially in the Permian and Mesozoic when they were the lords of creation.

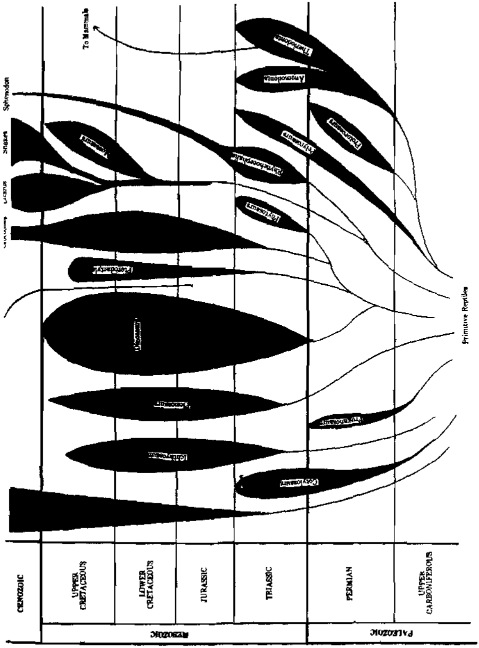

FIG. 121.—Diagram showing the relationships, relative abundance, and known geologic history of the Reptilia. (*After Gregory.*)

Their fundamental structure will first be considered in somewhat more detail than was done in the case of the Amphibia. Reptiles are cold blooded; naked, with horny, scaly, or bony armor; breathing exclusively by means of lungs; with a com-

pletely ossified skeleton, the skull articulating with the backbone by a single occipital condyle. Typically with two pairs of limbs, which exhibit a great variety of modifications due to adaptations to different habits of life, such as running, swimming, flying, etc., and practically absent in the snakes. Reptiles exhibit a much greater diversity than the Amphibia and fully equal the diversities found in the Mammalia. Some of the dinosaurs are the largest known terrestrial animals.

Although particular parts of the skeleton of reptiles may be highly specialized for particular functions, the skeleton as a whole is much more generalized than the skeleton of a mammal.

In the most primitive reptiles the skull consists of 72 bones, and evolution of this part of the skeleton has consisted chiefly in the reduction of bones either by consolidation or disappearance. Counting the tiny bones in our ears, the human skull consists of but 28 bones. These ancient reptile skulls have a continuous bony roof like that of a stegocephalian amphibian, perforated only by nostril, eye, and pineal openings. In the modified reptiles the region back of the orbits (temporal region) has one or two open spaces (temporal fossæ or vacuities) which have developed along different lines and constitute important clues to relationships.

In these ancient reptiles—Labidosaurus (Fig. 122[4]) of the Permian, for example, the lower jaw consisted of 14 bones—7 to each of the two mandibles. In mammals the lower jaw consists of a single pair of dentary bones, and in those reptiles (theriodonts) which are considered to represent the Permo-Triassic ancestors of the mammals, all of the jawbones except the dentary are very greatly reduced. The teeth of reptiles are indefinite in number and may be attached to any of the palate bones. Except in those reptiles ancestral to mammals (theriodonts), they are nearly alike throughout (homodont) and are not differentiated as are the teeth of mammals; hence, the teeth of reptiles, as a rule, are not very important clues to relationships. They may be inserted in sockets or in grooves or coossified with the surface of the jawbones.

They are usually replaced indefinitely by new teeth growing from the side or below. They are generally conical and curved—those of carnivorous forms being somewhat compressed with sharp fore and hind edges, those of the herbivorous forms with somewhat dilated and roughened crowns. Except in certain of

the dinosaurs they never have but one root. The backbone is always ossified, although remnants of the notochord may persist in the vertebral centra. The number of vertebræ is highly variable (30 to 500) and there is usually not much regional modification from neck to tail, although the vertebræ do show many adaptational modifications. Originally, all the vertebræ had at least traces of ribs. The earlier reptiles have vertebræ

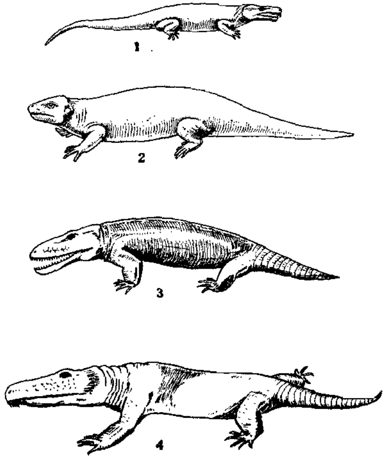

FIG. 122.—Restorations of various Cotylosauria. (*After Williston.*) 1. Limnoscelis. 2. Diasparactus. 3. Seymouria. 4. Labidosaurus.

with concave centra like those of fishes, affording great flexibility of bodily movement but not very great strength. This type of vertebral articulation is still found in the existing geckos and in tuatera (Sphenodon). Most later reptiles have the centra concave in front and convex behind, but in some extinct Mesozoic forms (some of the dinosaurs) the centra are convex in front and concave behind.

The ribs were at first slender and curved with a single articular head. Later, they became double headed, as is the rule among

mammals. Still later, they became greatly modified. Thus, in the lizards (Squamata), the original head (tubercle) disappears and the second head (capitulum) is all that remains. In other groups, the place of attachment to the vertebræ became altered in various ways.

The ventral ribs are slender ossifications in the tissues on the underside of the body and are characteristic of most reptiles. The front ones become fused to form a breastbone (sternum) which was otherwise absent in the earlier reptiles. The shoulder (pectoral) girdle consisted, originally, of the following six bones: scapula, coracoid, metacoracoid, clavicle, interclavicle, and supraclavicle or cleithrum—the last vestigial and an inheritance from the Amphibia. The first five of these are present in the most primitive living mammals (egg-laying monotremes). The metacoracoid has disappeared and the clavicle is often absent in living reptiles. The hip girdle or pelvis consists of three pairs of bones (ilium, ischium, pubis, composing the innominate bone), as in birds and mammals, and these are often intimately fused in adults.

The limbs are greatly modified according to the habits of their owners, becoming adapted for walking, running, burrowing, climbing, swimming or flying, and will be considered in the particular reptiles selected to illustrate some of these adaptations.

The oldest known reptiles appear in the Upper Carboniferous. While the Amphibia were adapting themselves to the variety of habitats of the coal swamps, coastal lagoons, and seasonal water pools on the land, certain of the solid-headed (Stegocephalia) forms gave rise to the first reptiles. The actual transitional forms are not known, but the ancestral reptile may be pictured as lizard-like in appearance, a dweller in a warm, terrestrial, dry environment favorable to bodily activity, which, in turn, reacts on the development of a nervous system. Such an environment necessitates a certain amount of alertness in the securing of food and the development of claws on the fingers and toes. From some such ancestor there was a rapid adaptional spread of the reptiles over the land surfaces of the earth contemporaneous with the final flowering of the various stegocephalian groups of Amphibia during Permian time. Some of these Amphibia survived in considerable numbers into the Triassic, notably the labyrinthodonts, but they are entirely overshadowed by the great variety of Triassic reptiles—the Triassic reptile

faunas comprising not only relatively little-changed survivors of the Permian cotylosaurs, pelycosaurs, anomodonts, and theriodonts but also new evolutionary products representing all of the wonderfully diversified Middle Mesozoic terrestrial aquatic and aerial reptiles.

None of the later reptilian orders is missing in the Triassic except the stock which gave rise to the Cretaceous mosasaurs and the modern lizards and snakes. In no case is it supposed that the actual oldest known fossil of any of these stocks represents their first appearance, and that is why the ancestral lines are carried back much farther into the past. It is known that the beginnings of these various lines were more ancient because of the time required to evolve such diverse reptiles as the turtles, crocodiles, dinosaurs, and the flying forms or such a complete adaptation to marine life as were the ichthyosaurs. Permian reptiles represent five different orders—the cotylosaurs, proganosaurs, pelycosaurs, protorosaurs, and the theriodonts, much alike in some of their members and highly unlike in the specialized forms.

The cotylosaurs, of which several restorations are shown (Fig. 122), were lizard-like in appearance and scarcely distinguishable from some of the Amphibia, on the one hand, and many Reptilia, on the other. The skeleton, however, was extremely primitive, notably the solid skull—the bones of which contain all or most of the elements found in a stegocephalian skull, as do the elements that make up the jaws. They show adaptations for a wholly terrestrial existence, as in Pantylus, Diadectes, Chelonyx, and some of these develop a partial armor of bony plates. Others, like Labidosaurus, were partly aquatic, and others, like Limnoscelis, were more fully aquatic. They all became extinct during the Triassic.

The proganosaurs were aquatic adaptations, probably from the common ancestry of the cotylosaurs. Both the neck and the tail became lengthened and the skull shows a single pair of temporal openings.

The Protorosauria have a single pair of temporal openings, an elongated neck, and hollow bones. The genus Protorosaurus, itself of the Permian, was strictly terrestrial. Williston has described a similar but more completely preserved form (Aræoscelis) from the Permian of Texas. Aræoscelis had a long balancing tail, slender body, five long, clawed fingers and toes, and was

probably a climbing form. Other protorosaurs (Pleurosaurus) were aquatic and swam much like eels. The group as a whole

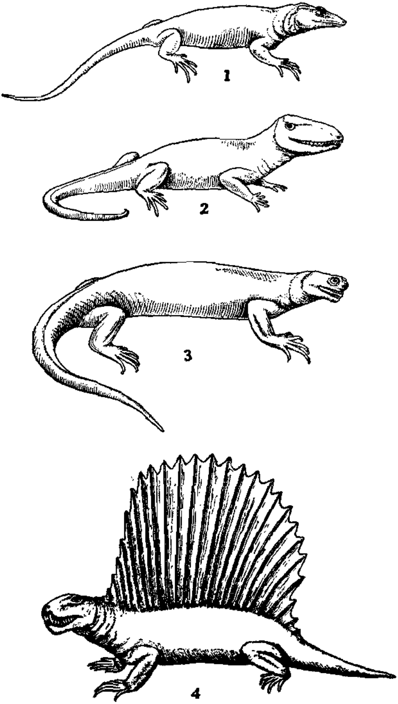

FIG. 123.—*Restorations of various Pelecyosauria.* (*From Schuchert, after Williston.*) 1. Varanosaurus. 2. Casea. 3. Ophiacodon. 4. Dimetrodon.

is not well understood, and some students think that it may have represented the ancestors of the much later lizards. As at present understood it became extinct in the Permian.

The pelecyosaurs in their more primitive forms look much like cotylosaurs, as may be seen from the accompanying restorations (Fig. 123), and in their skeletons these earlier ones much resemble the protorosaurs, but they have two pairs of temporal openings (what osteologists term "diapsidan"). They were mostly terrestrial, active, carnivorous, and predatory, with short, strong, five-toed legs; but a few became adapted to a semiaquatic or swimming existence. The earlier had flat skulls and simple teeth, the later had high skulls and some differentiation of teeth, especially at the front of the jaws. Their most remarkable specialization, which has given them the popular name of "finback lizards" (Dimetrodon, Clepsydrops, Edaphosaurus), was the progressive lengthening of the spines (neural) at the top of the vertebræ, some of which (in Dimetrodon) reached a length of over 3 feet and supported a membranous fin. In some, these bony rods were smooth, but in Edaphosaurus they developed peglike side growths. It is not certain whether these spines were defensive or purely ornamental, originating by sexual selection, but it seems certain that this bizarre specialization was what brought the pelecyosaurs to extinction toward the close of the Permian.

The fifth Permian group—the theriodonts and anomodonts evolved in another life province (South Africa), where continuous continental deposits extend from Permian through Triassic and yield a remarkable array of these strange extinct beasts, which are sometimes so like mammals in structure and habits. They vary greatly in size, structure, and habits, some large, some small, some slow, some fast, some partly armored. They include herbivorous, omnivorous, and carnivorous forms, some with their jaws toothless and encased in a horny beak like that of a turtle (anomodonts, Fig. 124[1]), others with teeth suggesting those of a mammal (cynodonts). These last are especially characteristic of the Triassic and give us a picture of how mammals originated, although the known fossil forms are probably not the direct ancestors of the mammals.

Such a form as Cynognathus, (Fig. 124[2]), 5 or 6 feet long with a large head, stout body, and stout tail, had the three pairs of pelvic bones united to form the innominate bone as in mammals—a feature not found in any other reptiles—the teeth had become differentiated into incisors, canines, and molars, as in mammals, the lower teeth biting inside the upper and the lower canines

biting in front of the upper, as in mammals; the limbs were also mammal-like in structure and appearance; and there is an approach to the double articulation of the skull and spinal column (double occipital condyles) which characterizes the mammals. Whether any of these reptiles became warm blooded is not known; perhaps this change to a four-chambered heart and increased body temperature, and the corresponding influence on brain evolution, may mark the boundary between reptile and mammal that was passed by some as yet unknown form in late Permian or early Triassic times.

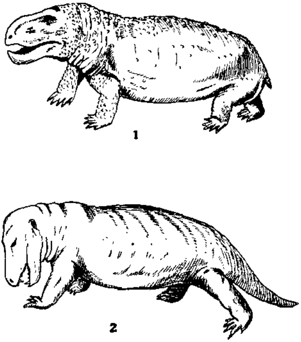

FIG. 124.—Restorations of 1. The Permian turtle-jawed Anomodont, *Endothiodon*. 2. The Triassic dog-toothed Cynodont, *Cynognathus*. (*After Gregory*.)

RHYNCHOCEPHALIA

The name comes from the two Greek words meaning "snout headed." It is used in somewhat diverse ways by different students of reptiles, the older naturalists including the protorosaurs, proganosaurs, and pelycosaurs in this group, which, in consequence, was considered to go back to the late Carboniferous. In their ancestry these three groups are undoubtedly closely related but the rhynchocephs, as here defined, comprise only the abundant Triassic forms which continue to the present in the case of the single genus Sphenodon (Hatteria) of New Zealand, which lives on beaches, hiding among the rocks and only occasion-

ally venturing into the water. Sphenodon, or *tuatera*, as it is locally called, 2 feet or under in length, was always thought to be a true lizard (Lacertilia) until about 40 years ago, but despite its external resemblance to the true lizards, its internal structure is very old fashioned, especially in the skull, which is diapsidan with primitive jaw articulations, an immovable quadrate, and biconcave vertebræ with persistent intercentra.

The Rhynchocephalia comprise three groups—the Sphenodontidæ, including the living Sphenodon and various extinct genera going back to Upper Jurassic; the extinct Rhynchosauridæ of the Triassic; and the Champsosauridæ or Choristodera of the late Cretaceous and early Tertiary. These last were moderately sized—not more than 4 or 5 feet long and were partly aquatic, perhaps to the extent that a modern alligator or crocodile is aquatic. They had slender bodies, long, slender faces, and a flattened swimming tail. Although the notochord no longer perforated the vertebræ, the latter were very shallowly biconcave. The bones of the palate retained teeth—a primitive feature—and the first vertebræ were also old fashioned and suggestive of Paleozoic conditions, as was also the structure of the pelvis.

The Champsosauridæ appear to have originated in North America in the late Cretaceous and spread as far as Europe in the early Eocene, but compared with all the other reptile stocks theirs was short lived and, by this standard, not especially successful.

Little is known of the geological history of the true lizards or snakes and the chief interest of reptile evolution during the Mesozoic lies in the assumption of flying habits by the pterodactyls; the various adaptations to aquatic life in many reptile stocks; and the evolution of the most abundant and dominant terrestrial reptiles—the dinosaurs. Since but one order—the pterodactyls or Pterosauria—attained flight, and the dinosaurs represent but a single or perhaps double-evolving stock, we may pause to consider briefly the nature of the adaptations to an aquatic life, since they occurred in so many unrelated lines.

These habits generally proceed from terrestrial to swamp living (palustrine); to lake, lagoon, and river inhabiting; to shallow marine habitats; and, finally, to pelagic oceanic forms like the plesiosaurs and ichthyosaurs, the latter even spared the necessity of resorting to the shores to lay their eggs, since, in the Jurassic ichthyosaurs, at least, the eggs are hatched in the body of the

mother and the young are born alive and free swimming. As the land became overpopulated, diverse kinds of animals sought safety or food in a return to a partly or wholly aquatic existence. Such aquatic adaptations from terrestrial ancestors have occurred repeatedly among many different orders of reptiles.

These aquatic adaptations, partially or wholly acquired, consist in an elongation of the face, with long jaws armed with numerous sharp, slender teeth—adaptations for catching their food, which consists predominantly of fishes. The external openings of the nostrils tend to move back from the end of the snout—their position in terrestrial reptiles—toward the eyes. This is not true of modern crocodiles but is, nevertheless, usual in other groups. The neck tends to elongate as in the proganosaurs and plesiosaurs. Generally, but not always, those with long necks have short tails; those that have short tails not efficient for quick turns in pursuit of their prey have long necks, and this is also due to the sinuosity of body movement in swimming. The trunk generally becomes more slender and the tail tends to become compressed. This modification reaches its extreme specialization in the later ichthyosaurs which have a tail like a fish.

Terrestrial animals must have firmly articulated joints. Among aquatic forms there is a tendency to looseness of joints, compensated for by increasing flexibility. The most striking modifications are seen in the limbs which usually loose all resemblance to the legs of terrestrial forms and become paddles or flippers. Those in which the tail is the chief organ of propulsion use their modified limbs for balancing and turning, and the front pair tend to be larger and to be retained, when, perhaps, the hind pair have become vestigial. Those that use their legs for propulsion tend to have the hinder pair better developed. The limb bones become shorter in the tail swimmers like the plesiosaurs and ichthyosaurs and longer in the limb swimmers, and new phalanges are added (except in turtles). The actual substance of the bones becomes more spongy. Another aquatic adaptation is the ossification of the sclerotic membrane of the eye to protect the cornea and accommodate the soft parts to varying pressure.

Aquatic reptiles also tend to dispense with the horny scales or bony plates which afford protection for their terrestrial relatives. Since these and other modifications are adaptations to

an aquatic existence, it follows that diverse stocks which become adapted for this mode of life tend not only to look alike but to modify their skeletons as well, so that it is often puzzling to make out their real relationships.

Plesiosauria

The name plesiosaur is from the Greek, meaning "like a lizard" —a not very appropriate name—and the first one was described only a little over 100 years ago, although their fossil bones are often exceedingly common in the long-settled parts of Europe. They are exceedingly numerous and varied and it is only in recent years that their structure has become at all well known.

The term Sauropterygia, from the Greek meaning a "lizard with fins," is now usually applied to the group in place of the more familiar term of Plesiosauria. Dean Buckland, the eminent author of the famous Bridgewater Treatise (1836), likened a plesiosaur to a snake threaded through the shell of a turtle and the simile is not at all bad, for most of them have a stout body and an inordinately long neck. They are almost perfectly adapted for oceanic life but their adaptation is along quite different lines from that in the ichthyosaurs, turtles, mosasaurs, and extinct oceanic crocodiles—the four other groups that, in whole or on the part of some of their members, lead pelagic lives. Some of the plesiosaurs are relatively the longest-necked animals of either the past or the present, with as many as 76 neck (cervical) vertebræ. No mammal has more than 9 neck vertebræ, and 7 is the rule, and long-necked mammals like the giraffe get the length by the lengthening of the 7 neck vertebrae. Birds lengthen their necks both by lengthening the individual vertebræ and by increasing their number up to 21. All plesiosaurs were not long necked, some having necks shorter than their heads, instead of twelve times as long, and may have as few as 13 neck vertebræ.

The longest-necked plesiosaur is a species of Elasmosaurus (Fig. 125[3]) which had the following dimensions: head 2 feet, neck 23 feet, body 9 feet, tail 7 feet. The shortest-necked one is a species of Brachauchenius which had a head 2½ feet long, a neck less than 2 feet long, and a body about 5 feet long. In fact, it is well to remember that there were a great many different kinds of plesiosaurs. Upward of 100 kinds are known, and this

is probably not more than a third of the number that lived during the Mesozoic.

The nearest approach to an ancestor of the plesiosaurs is a group of semiaquatic reptiles found in the Triassic of Europe and known as "nothosaurs" (Fig. 125[1]). They are much smaller than the true plesiosaurs, the largest less than 10 feet in length, with a moderately long neck of about 20 vertebræ, a slender body, and a relatively long tail; the legs were long and the fingers and toes, though somewhat flattened and probably webbed, had not

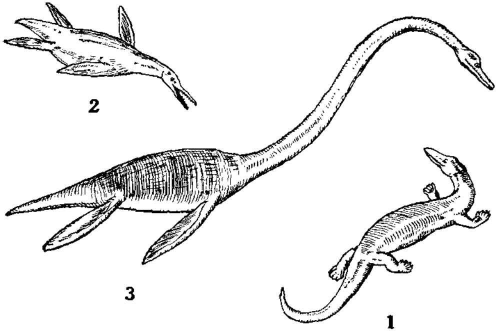

Fig. 125.—Restorations of nothosaur and plesiosaurs. (*After Williston.*) 1. Lariosaurus, a Triassic nothosaur, one-twentieth life size. 2. Trinacromerium, a short-necked Upper Cretaceous plesiosaur, one-eightieth life size. 3. Elasmosaurus, a long-necked Upper Cretaceous plesiosaur, one one-hundredth life size.

yet been modified into paddles, the finger and toe bones being of the normal number. They doubtless spent much of their tim in the water about the shores of the Triassic sea (see restoration o Lariosaurus, Fig. 125[1]). The earliest known true plesiosaur occur in the Lower Jurassic. In these the legs had becom modified into paddles by the shortening of the bones and a increase in the number of finger and toe bones. In the late Upper Cretaceous plesiosaurs, all of the bones beyond the stou upper arm and upper leg bone were much shortened, those o the wrists and ankles are similar polygonal bones, and the finge

and toe bones are still more numerous, sometimes as many as 24 in each digit (Fig. 126).

The plesiosaurs may be pictured as having stout, broad, and flat bodies, with a smooth skin which had lost its scales (this is known because impressions of the skin have been fossilized). The front and hind paddles were equally developed and alike, showing that they were the main organs of propulsion, the tail

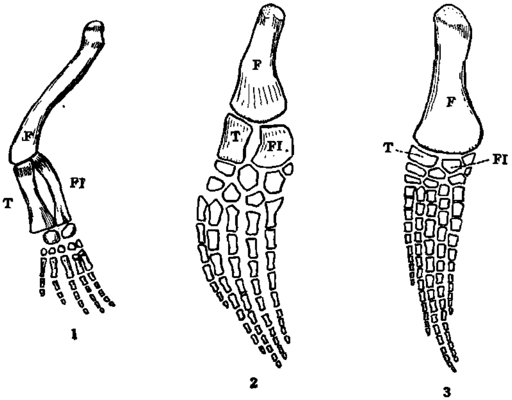

FIG. 126.—Showing the evolution of the leg bones in the plesiosaurs. Left hind leg of 1. Lariosaurus, a small Triassic nothosaur. (*After Fraas.*) 2. Thaumatosaurus, a Lower Jurassic plesiosaur. (*After Williston.*) 3. Trinacromerum, an Upper Cretaceous plesiosaur. (*After Williston.*) *F*, femur; *T*, tibia; *FI*, fibula. Not drawn to scale.

being relatively short. Their heads were mostly small and the jaws long and slender and armed with sharp conical teeth in sockets. The largest teeth that have been found are about 4 inches long. The jaw structure shows that the plesiosaurs were strong biters and tore their food as a crocodile does instead of swallowing it whole as does a snake. Probably, fishes were the chief item on their menu, although doubtless any other animal food, living or dead, was utilized. They swallowed pebbles in the same way that crocodiles do, and plesiosaurs have been found fossil in Kansas with pebbles inside them that must have

been picked up in the Black Hills region, showing that they swam long distances. Whether they were as truly oceanic as the ichthyosaurs and brought forth their young alive instead of having to resort to the shores for hatching their eggs is not absolutely certain but is very probable. Fossil embryos and young forms have been found fossil but never inside their mothers, as is sometimes the case in the ichthyosaurs. For some as yet unknown reason, they became extinct before the close of the Upper Cretaceous, although they seem to have been well able to cope with any conceivable enemies they may have had, and it is hard to imagine any environmental change which would have brought about their extinction, for they ranged over the whole earth and their fossil remains have been found in marine deposits on every one of the continents.

Ichthyosauria

The ichthyosaurs are the supreme adaptation of the reptile to an oceanic life and deserve the term "sea rovers" quite a much as do modern dolphins. The name means "fish reptile,' and many of the older naturalists thought that ichthyosaur were fishes, just as many of the later naturalists thought then to be descended directly from fish ancestors. They are s perfectly adapted for marine life that, although we kno their skeletons in detail and the outlines of their soft part even today we cannot be sure of their precise relations to othe reptiles or their precise ancestry, though it is certain that th ancestry started on the land. The proof is too long to be give here but we can appreciate that we are dealing with modificatio by adaptation for it is the latest ichthyosaurs that are mo fishlike and not the earlier, which are more like normal reptile Structurally, the ichthyosaur is entirely reptilian notwithstandi its fishlike form and habits, and it seems that it is among t cotylosaurs and proganosaurs of the earlier reptiles that we mu search for their actual ancestors.

The ichthyosaurs were from 2 to 30 feet long, with lon slender jaws armed with numerous, rather small, sharp, conic recurved teeth set in grooves and admirably adapted for seizi active slippery prey. The nostrils were far back near the en mous, alert eyes, which had a correspondingly large sclero ring of bony plates. The neck was short, no more obvious th

the neck of a fish, and capable of but slight movement. The body was slender. The tail was compressed with a fleshy fin, which, in the later forms, resembled that of a shark (it will be seen later how this originated). There was also a dorsal fin like that of a shark (a fish) or a dolphin (a mammal), and this feature is unique among reptiles.

The limbs are much more modified than in the plesiosaurs and had a wider range of movement. As in the fins of a fish in which the tail is the chief organ of propulsion, the front pair gradually become much larger than the hinder and are used chiefly for balancing and quick turning. This gradual disuse of the hind legs resulted in their decrease in size and is reflected in the weak pelvis and the loss of the sacrum. If the ichthyosaurs had not become extinct for some unknown reason during the Upper Cretaceous, we can confidently predict that by this time they would have lost all traces of hind legs, as have the existing whales.

The ancestral limb bones gradually dissolved, as it were, into numerous bony disks for the support of the paddles. In the Triassic ichthyosaurs, the paddles were still used for propulsion, consequently, they were larger, more nearly of a size, and with longer bony elements. In the later forms, the elements increased greatly in number and became short and similar, and some forms show as many as ten digits. The vertebræ were deeply biconcave—an adaptation for flexibility. The ribs were numerous, long, and slender.

Most interesting was the modification of the tail. In the Triassic ichthyosaurs, like Cymbospondylus from Nevada or Mixosaurus from Spitzbergen (Fig. 127[1]), it was long and slender with a relatively narrow marginal fin. As the tail was used more and more for swimming, it shortened and the fin shortened and heightened at the end of the tail which was bent down into the lower fin lobe. Figure 127[2] shows the proportions and arrangement in a Lower Jurassic form. By Upper Jurassic time, the tail had become symmetrical and the fin was a highly effective and nearly symmetrical vertical affair strengthened by the reduced caudal vertebræ (Fig. 127[3]). This series of modifications brought about by the mechanics of swimming is closely parallel to the earlier evolution of the tail fin in the fishes.

The later ichthyosaurs were very active predaceous animals world-wide in their distribution. Fossil food found within

the ribs in the place where their stomach was located as well as a study of their fossilized excrement shows that their food consisted largely of fishes, squids, and those fossil squids known as "belemnites." These all left recognizable hard parts, and doubtless other invertebrates which have left no traces were also eaten.

The general trend of ichthyosaur evolution may be summarized as a shortening of the body, especially of the neck and tail; an increase in relative size of the head and a lengthening of the jaws; increase in size of eyes; and a shortening of the vertebræ; a change from teeth in sockets to arrangement in grooves; an

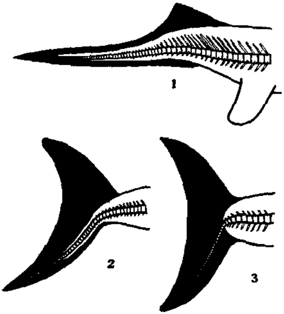

FIG. 127.—*Showing the evolution of the tail in the ichthyosaurs.* 1. *Mixosaurus* of the Triassic. (*After Wiman.*) 2. Ichthyosaurus of the Lower Jurassic. (*After Abel.*) 3. Ichthyosaurus of the Upper Cretaceous. (*After Bauer.*)

increase in the forward paddles and a decrease in the hind paddles with the corresponding change in the bones from those resembling terrestrial reptiles to the multiple-boned flippers of the more specialized forms.

The most interesting of their adaptations to marine life (not even attained by sea-going turtles) is the habit of bringing forth their young alive, a visit to shores to lay their eggs being consequently not necessitated. Embryo ichthyosaurs have rather frequently been found fossil inside their mothers, as many as seven in one instance, and that they represent prenatal young and not food is indicated by the uniform size of the embryos and the fact that they belong to the same species as that in which

Fig. 128.—Restoration of a mother ichthyosaur and young. (*After Knight.*)

they were found. If this rested on a single specimen we might be skeptical and some of the smaller skeletons inside larger ones may represent prey, but it cannot be true of all, and the above explanation is fully warranted, especially as the attitude of some of the little ones indicates that they were still enclosed in the egg sac.

The abundance of ichthyosaur remains in some localities and their absence from others warrants a belief that they were gregarious like the present-day dolphins and porpoises (mammals). They appear as fossils in the Middle Triassic, and doubtless some day their less modified ancestors will be discovered in the Permian. They reached their maximum during the Jurassic and became extinct shortly after the dawn of the Upper Cretaceous, earlier than the plesiosaurs or mosasaurs, showing that this extinction was not due to any general environmental cause which would have equally affected their contemporaries.

The restoration of a mother ichthyosaur with five young copied from Knight's well-known painting will emphasize the fishlike form and habits and serve to vitalize the features that have been described (Fig. 128).

Parasuchia

The phytosaurs, united with the crocodiles by Huxley, are now considered a separate order, Parasuchia, with three suborders—the Phytosauria; the Ætosauria, small, terrestrial, armored forms; and the Pelycosimia, Lower Triassic terrestrial forms from South Africa.

The phytosaurs were of considerable size and greatly resembled crocodiles in both form and habits; in fact, their structure shows this relationship, differences being the backward position of the nasal openings, the absence of a false palate, and the more primitive shoulder girdle. Their jaws were long and narrow like those of a modern gavial, and the skin developed bony plates. The name *phytosaur* means "plant lizard," mistakenly given by Jæger in 1826, for these animals were undoubtedly carnivorous. Their race was short lived, coinciding with the Triassic period. Their remains have been found in North America, Europe, Africa, and Asia, and the most familiar genera are Belodon, Rhytidodon, and Mystriosuchus.

Crocodilia

The Crocodilia surviving in the present comprise the crocodiles, alligators, gavials and caimans, numbering in all about 25 species, the sole living representatives of an ancient line going back to the late Triassic and culminating during the Mesozoic. They all belong to the latest of the three suborders into which the order is now divided—the first being the Eusuchia, meaning "true crocodiles." Formerly, they were considered related to lizards, but this is not the case.

The suborder Eusuchia have broad, flat heads, flat bodies, and narrowed, long tails, the tail being the chief swimming organ, although the toes (five in front, four behind) are more or less webbed. The legs are rather of the terrestrial type, that is, relatively long, and the animals are perfectly at home on the land. The body is covered with horny scales beneath which are a larger or smaller number of bony plates. The lower jaw articulates with the cranium on quadrate bones which are firmly fixed and not movable, as in the lizards and snakes. The bones of the palate or roof of the mouth are firmly united and by outgrowths of bone from the sides below the nasal chambers form a false palate, so that there is an enclosed canal from the external nasal openings at the front of the snout, and the animal breathes through its nose like a mammal instead of through its mouth as in all other reptiles except the immediate ancestors of the mammals. The teeth are conical, firmly set in sockets, and variable in number. The vertebræ (with the exception of three of them) are concave in front and convex behind. The crocodile-alligator-caiman group appear in the Upper Cretaceous and include broad- and narrow-snouted forms. In the early Tertiary, some, like the modern alligators, reached a length of 50 feet. They survive in over 20 species found in southern Asia and in warmer parts of North and South America, Africa, and Madagascar, and were much more widespread during the Tertiary.

The second surviving group comprises the Tomistoma or long-snouted crocodiles. These appear, also, in the Upper Cretaceous and survive in two species found in Borneo.

The third group includes the gavials with extremely long and slender snouts. They appear in the Tertiary and reach lengths of 50 feet in the Pliocene of India. They also survive in two species in the rivers of southern Asia and are more strictly aquatic than the familiar crocodile-alligator group.

The suborder Mesosuchia, meaning "middle crocodiles," are rather more closely related to the Eusuchia than was formerly supposed. They comprise a variety of extinct forms extending from the lower Jurassic to the beginning of the Tertiary and their chief structural difference is their more old-fashioned vertebræ, which were biconcave. The internal opening of the nasal passages is not so far back in the mouth as in the Eusuchia, and they were more completely armored. The earliest Mesosuchia are all long, narrow-snouted forms known as "teleosaurs," but toward the close of the Jurassic, broad-snouted forms, mostly of small size, make their appearance, and both kinds in diminishing numbers continued through the Cretaceous.

The name Thalattosuchia of the third suborder, translated from the Greek, is "sea crocodiles" and appropriately describes the abode of these ancient beasts, which differed so considerably in both habits and structure from their mostly later relatives

FIG. 129.—Restoration of Geosaurus, an Upper Jurassic sea crocodile.

of the two preceding suborders. They were a relatively short-lived race, the few known forms all coming from the late Jurassic deposits of Europe. The part they played in the organic history of the earth is a very minor and obscure one, and their chief interest is in the record they preserve of a scene from the distant past, of river dwellers like the gavial of the Ganges venturing farther and farther out to sea in pursuit of food and gradually becoming wholly aquatic—their skins losing their now useless armor, the eyes becoming furnished with a ring of sclerotic bones (not found in any other crocodiles), their teeth becoming still better adapted for catching fish, their bodies lengthening, the dorsal and ventral processes of the tail vertebræ becoming enlarged and compressed and supporting a vertical fin, and the front legs becoming modified into incipient paddles. Possibly, their failure to acquire the habit of bringing forth their young alive and the consequent necessity of seeking the shores for egg laying was the reason that caused their hind legs to retain most of their terrestrial features and was the real reason for the inability of the thalattosuchians to stand the competition of the ichthyosaurs and plesiosaurs.

Pterosauria (or Pterodactyls)

We now come to one of the most interesting groups of reptiles, appropriately called the "dragons of the air," not that they were formidable like the dragons of mythology, but because of their, to us, uncanny appearance and the large size of some of them. Only three other groups of organisms have become adapted for sustained life in the air—the insects among invertebrates, the birds, and the bats among the mammals. Many others have developed incipient or gliding flight, like the flying squid, the little lizards of the Indo-Malayan region (Draco) in which five or six pairs of ribs are extended from the sides and are connected by a membrane or fold of skin, the flying squirrels and flying foxes, and the so-called "flying snake" and "flying tree frog" of Borneo. None of these really flies but sails or glides imperfectly in the case of the snake and frog or more perfectly in the case of the others mentioned, like a man with a glider or parachute. All depend on the initial take-off, the sustaining action of the air current set up, and gravity. The adaptation in the case of the flying fish, so much disputed, is a step beyond any of these, since their vibrating fins must furnish some, if but slight, motive power.

The pterodactyls, however, are in a class by themselves among all the Reptilia in having solved the problem of true flight somewhat earlier than the birds and in having been able to travel long distances from shore, since their bones are found abundantly in marine deposits mixed with those of fishes, ichthyosaurs, plesiosaurs, and mosasaurs. They appear suddenly in the record in the late Triassic, of unknown ancestry, become abundant in the Jurassic, and disappear at about the middle of the Upper Cretaceous, showing in all this lapse of time but slight structural changes other than increase in size, loss of tail and teeth, and some mechanical improvements in the shoulder girdle.

They ranged in size from that of a swallow to larger than any existing birds—the gigantic pteranodon shown in the accompanying restoration (Figs. 130[1] and 131) could cover a condor or albatross, our largest flying birds with one of its wings and commonly had a wing expanse of about 20 feet, and some specimens indicate that some individuals may have measured 25 feet from tip to tip. They are not at all closely related to birds, and their flight is more strictly comparable to that of the bats, with similar

membranous naked wings; only in the bat it is the elongated fingers of the hands which support the wings, whereas in the pterodactyls it is the tremendously elongated and strengthened little finger which gives them the needed support.

Although space does not permit a complete account of the different kinds of pterodactyls or of the structure of their skeleton, a few features may be given of adaptations similar to those in

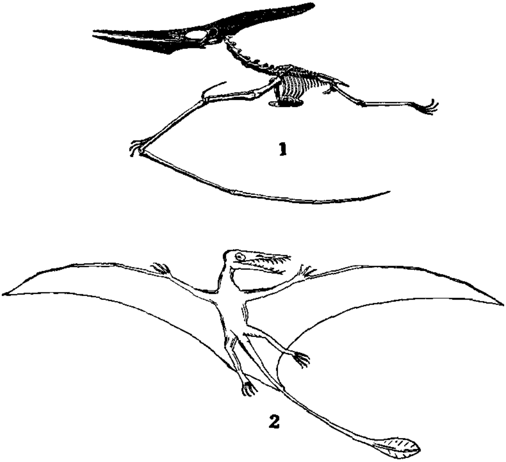

FIG. 130.—1. Skeleton of Pteranodon (*after Eaton*), one-fiftieth life size. 2. Restoration of Rhamphorhynchus (*after Marsh*), one-seventh life size.

birds and doubtless evolved in the same way but not indicating any real relationship. The bones were hollow and very light; the skull was articulated on the neck so that their axes were nearly at right angles; the jaws were long and slender; the orbits and, consequently, the eyes were large; there was a large breastbone (sternum), which, however, was without a keel; the fifth toe (absent in birds) was sometimes vestigial. On the other hand, the pterodactyls were naked, the vertebræ were concave-convex and biconcave and otherwise quite different from those

FIG. 131.—Restoration of the giant Pteranodon of the Upper Cretaceous of Kansas, about one-thirty-fifth life size. Modified from Cruikshank.

of birds; the quadrate bones were fixed; the shoulder girdle lacked clavicles; and the limbs were modified for flight along entirely different lines.

The thumbs are wanting in the hands and the fifth toe is sometimes modified or reduced; all the other fingers and toes except the enormously elongated little fingers are clawed. The earlier pterodactyls had long tails and in Rhamphorhynchus of the Upper Jurassic (see restoration) its end was expanded into a keel for steering and turning purposes. In the later forms the tail became much shortened or disappeared altogether.

In pteranodon (see restoration, Fig. 131) which was probably the most specialized of the pterodactyls as well as the largest known flying animal of the past or present, everything seems to have been sacrificed for food and flight; the teeth had disappeared, the body was slender and is estimated to have weighed not more than 25 to 30 pounds, the skull is very narrow and extended backward nearly as far as the jaws did forward and probably served as a counterpoise for the jaws and as an aid in steering.

Pterodactyls were of all sizes and doubtless varied in food and other habits. The smaller probably chased insects as do the bats; the larger are supposed to have been mainly fish eaters. When resting on land some may have hung from rocks and branches as do the bats and if they walked about much it would seem as if they would have had to go on all fours with their wings held aloft out of harm's way.

Chelonia (The Turtles)

The scientific name of this order, Chelonia, is the Greek word for "tortoise" or "turtle." This is the one order of reptiles so distinctive in appearance that any child would unhesitatingly recognize it in an assemblage of all the reptiles of the past or present. No order has a longer and more uneventful history and of none is the origin more obscure, although the anapsidan condition of the temporal part of the skull points to the cotylosaurs as the possible ancestral stock. Perhaps the cotylosaur Tunotosaurus of the Permian, with its flattened, platelike ribs, may represent such an ancestral type. The early cotylosaurs were all shore or marsh animals and more or less aquatic. The oldest known turtles—Proganochelys and Triassochelys of the Upper Triassic—as restored by Jækel (see Fig. 132) were as

turtle-like as a modern alligator snapper, which they resembled in structure and doubtless in habits, being equally at home in

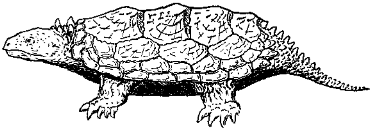

FIG. 132.—One of the earliest known turtles, Triassochelys, one-sixteenth life size. (*After Jækel.*)

the water and on the land, with the same toothless, horny, beaked jaws and the same plated armor.

The turtles are the only order of reptiles without any teeth or traces of teeth, so that their ancestors must have lost their teeth a very long time ago. Toward the close of the Jurassic, some of the turtles forsook the marshes, streams, and ponds where they had hitherto dwelt and went down to the sea, establishing that marine line represented by the modern leatherback (Sphargia or Dermochelys) of the warmer parts of the Atlantic, Pacific, and Indian oceans. At first they stayed in shallow waters but by Cretaceous times they reached their greatest size and only returned to the shore to lay their eggs.

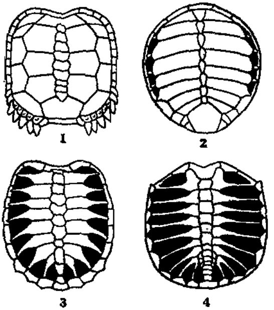

FIG. 133.—Showing the progressive reduction of the bones of the carapace in response to an aquatic life. (*From Swinnerton, after Fraas and Wieland.*) 1. Proganochelys from the Upper Triassic, one-seventeenth life size. 2. Thalassemys from the Upper Jurassic. 3. Toxochelys from the Upper Cretaceous. 4. Archelon from the Upper Cretaceous, one ninety-fifth life size. The open spaces between the bones are in solid black.

At the dawn of the Tertiary some of the turtles of the river plains migrated to the grasslands, developing into the land tortoises with their thick, completely closing, boxlike shells. These reached their maximum size in the late Tertiary. If the turtles were not so familiar and were entirely extinct they would be con-

sidered the strangest of reptiles and, perhaps, the strangest of vertebrates, for their shells are neither more nor less than the flattened and expanded backbone and dorsal and ventral ribs united with the associated bones and covered on the outside with horny skin plates, so that when a box turtle is seen to withdraw its head, feet, and tail inside its shell, it is really inside its ribs. In a newborn turtle the ribs are separate, as in other reptiles. With growth, the ribs begin to expand at their upper ends and then outward until their edges coalesce. In the sea turtles, which have less need for armor than those of the land or those that spend part of their time on the land, this is reversed and the continuous bony cover tends to disappear at the ends of the ribs and recedes toward the backbone, as shown in the accompanying diagram (Fig. 133).

The turtles are divided into the following four groups or suborders:

1. **Amphichelydia.**—These have biconcave neck vertebræ, a pelvis not united to the shell, and certain additional differences of no great importance in the skull and the arrangement of the plates of the undershell. They are wholly extinct and range from the Upper Jurassic to the Eocene.

2. **Pleurodira.**—The side-necked or snake-necked turtles, so called because the neck is long and when the head is withdrawn into the shell the neck is flexed sidewise. All are found in fresh water and all have clawed feet, although they are more or less webfooted. The pelvis is united to the shell. They appear in the Upper Cretaceous and are now confined to the Southern Hemisphere with about 40 species in South America, southern India, Africa, and Australia.

3. **Cryptodira.**—The snappers, marsh turtles, land turtles, and sea turtles. This is the most abundant group of living turtles, with about 150 species found on all the continents except Australia and including all the land turtles and the sea turtles of the warmer oceans. When the head is withdrawn within the shell, the neck is flexed vertically like the letter S. The pelvis is unconnected with the shell. They appear in the Lower Jurassic and include the largest living as well as the largest extinct forms. The sea turtles show a flattening of the shell with a loss of the horny skin plates and a partial loss of the bony tissue beneath. The front legs lose their claws and become strong flippers or paddles with a corresponding change in the shoulder

girdle designed to develop more power. They seek the shores for the brief period of egg laying.

The modern leatherback, in exceptional cases, attains a length of 6 feet which is only half that of the specialized giant among turtles—the Archelon of the middle of the Upper Cretaceous (Fig. 134). Archelon (restoration, Fig. 134, and diagram of carapace bones, Fig. 133[4]) to the number of several species is found in the interior Cretaceous sea of North America and the largest specimens were 12 feet long and weighed over 3 tons. The body was flattened (depressed), the neck short and not retractile. The bony plates had shrunk to the proportions shown in the diagram, and the dermal horny plates were gone except over the spine. The horny beak was strongly curved and the front legs were elongated and enlarged into highly efficient paddles. Expert opinion differs as to its food and whether it was sluggish or an active swimmer.

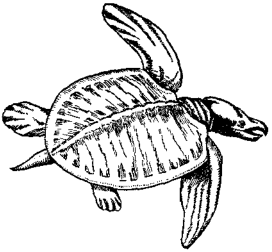

FIG. 134.—Restoration of the giant sea turtle Archelon, about one-seventieth life size. (*After Williston.*)

The land turtles which originated at the close of the Cretaceous have a highly convex thick shell which they can close when head, feet, and tail are withdrawn. They have legs adapted for walking. The highly arched shell is mechanically much stronger than a low arched one and prevents their being crushed by enemies and also accomodates an increased lung capacity.

4. **Trionychoidea.**—The mud turtles and river turtles, get their name from the fact of their having three claws retained on their webbed and paddle-like feet. They appear early in the Upper Cretaceous and they are almost exclusively aquatic; hence, they have flat, elliptical bodies, with long necks and small heads. The shell is incompletely ossified and lacks bony marginal plates. It is covered with smooth skin instead of horny skin plates. The neck bends vertically and the pelvis is free as in the Cryptodira. About 75 fossil species have been described and there are about 30 living species, chiefly in the Northern

Hemisphere but found on all of the continents except South America and Australia.

SQUAMATA (LIZARDS, SNAKES, AND MOSASAURS)

These constitute the order Squamata, from the Latin word for "scales," because the skin is usually covered with overlapping horny scales. They comprise the vast majority of living reptiles and are distinguished from all others in having movable quadrates—that is, a pair of bones to which the lower jaws are articulated in the Reptilia; hence, there is some freedom of movement

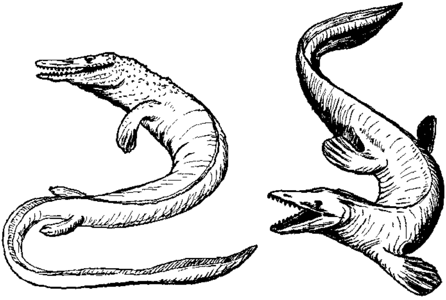

FIG. 135.—Restorations of two Upper Cretaceous mosasaurs. 1. Nectoportheus, one seventy-fifth life size. (*After Knight.*) 2. Clidastes, one twenty-fifth life size. (*After Williston.*)

forward and backward as well as sidewise. It has been thought that the Squamata were derived from the Rhynchocephalia but they are almost as ancient and the two groups were doubtless derived independently from ancestors like the protorosaurs or the more primitive among the pelycosaurs.

The palate is long and narrow and often bears teeth (a primitive feature). The vertebræ are generally concave in front and convex behind. The ribs are always single headed. The order is usually divided into four suborders—Ophidia or snakes and the structurally closely related; Lacertilia or lizards; Dolichosauria or extinct long-necked lizards of the Upper Cretaceous; and Mosasauria or extinct marine lizards of the Upper Cretaceous.

Suborder Lacertilia.—True land lizards somewhat like modern iguanas are found in the Triassic of South Africa (Paliguana) and must have been present from that time till the present, although their fossil remains are very rare except in the later rocks. There are upward of 2,000 existing species of lizards and they have become adapted to all sorts of habits—walking, running (especially in arid environments), living in trees (geckoes and chameleons), gliding through the air (Draco), living underground, amphibious, that is, partly aquatic (monitors), and aquatic (the sea lizard of the Galapagos Islands). Their skull shows important differences from that of the snakes, they generally have four legs, and they usually have movable eyelids and a non-protrusible tongue. The snakes have a more complete bony brain case, protrusible tongue, one lung, and no legs. Lizards are absent from the polar and subpolar regions and prefer warm climates. The majority of the lizards are small, graceful, and inoffensive, mostly carnivorous, the largest modern ones 4 to 6 feet long (some ignuanas and monitors).

Suborder Ophidia.—The number of living snakes is about 2,000 and their distribution is similar to that of lizards. They are mostly terrestrial, although at home in trees and in the water. Some are venomous, a relatively modern acquirement, and their habit of swallowing their prey whole is well known. They appear in the geological record late in Cretaceous time and their mostly terrestrial habits resulted in their relative rarity as fossils. A few are marine, like the sea snakes of the Indian Ocean in which the young are born alive, so that they never come on land. Snakes have lost their legs, although there are vestiges of the hind pair in some forms.

Suborder Dolichosauria.—An unimportant and imperfectly known group of Upper Cretaceous long-necked forms, which are referred to several genera and grouped in a single family. All are relatively small, under 6 feet in length, with slender bodies, and complete limbs and limb girdles. They were aquatic or semiaquatic and show a serpentiform adaptation in their shape and in their vertebral processes but were not ancestral to any existing lizards, all of which, except the monitors, have but 8 neck (cervical) vertebræ, whereas Dolichosaurus had 17 cervicals. They have been found in England and in southern Europe, although they may have been more widespread than we know.

since detached vertebræ are so like those of snakes that they are liable to be referred to the Ophidia. The dolichosaurs were a relatively short-lived race and became extinct before the close of the Upper Cretaceous.

Suborder Mosasauria.—Mosasauria derive their name from *Mosa*, Latin for the Meuse River, near which in Holland the first and most famous specimen was found, and *saurus*, a lizard. No other group of fossil reptiles is now better known, for they are abundant in the Upper Cretaceous chalk deposits of Kansas and other parts of the world—not only skeletons, but also stomach contents and impressions of the skin, sometimes preserving a part of their original coloration.

The Galapagos sea lizard (Amblyrhynchus) gives us a picture of the first change of habits in a terrestrial lizard on the way to becoming adapted for an oceanic existence. The sea lizard frequents the beaches and grows to a length of 3 or 4 feet. It has a compressed swimming tail and partially webbed feet, and obtains all its food in the shallow sea.

The Mosasaurs appeared at the beginning of the Upper Cretaceous in deposits in New Zealand and soon attained a world-wide distribution and died out just before the end of the Upper Cretaceous. Adults ranged from 8 to about 40 feet in length, with skulls 5 feet long. Their adaptation to marine life w s marked by the elongated, narrow, flattened skull, with sharp, curved, fish-catching teeth; by the backward position of the nostril; by bony ring of plates around the eyes, although the latter were smaller than in the plesiosaurs; by thick eardrums to resist changes of pressure when diving; by the short, strong neck and long tail; by the shortening of the arm and leg bones; a loosening of their articulations and the encasing of them in flesh and skin to form finlike paddles; and by the smooth skin covered with small scales.

The lower jaws just back of the teeth have a hingelike articulation permitting them to widen to admit swallowing fishes of large size—a unique feature which operated in the same way that the loosely joined flexible jaws of a small snake enable it to swallow a big frog.

Despite their size and marine habits, these ancient mariners differ less structurally from the existing monitors (Varanus) of Africa and Asia than the latter do from some contemporary lizards.

DINOSAURIA (THE DINOSAURS)

The name dinosaur is from the Greek, meaning "terrible lizard," but dinosaurs could not have been terrible except as regards the size of some of them, for they were stupid and slow—not governed by mind, since their brains were incredibly small. That is one of the reasons why the mammals completely displaced them at the dawn of the Tertiary. Nevertheless, throughout the whole Mesozoic they were the lords of creation on the land and the chief actors in the drama of terrestrial life, wandering to all of the continents and assuming a great variety of forms and habits. Some have thought that they may have become warm blooded but there is no evidence for this. Their fossil eggs were found in Madagascar years ago, a fact which seems to have been forgotten by most paleontologists, and more recently they have been found fossil in old sands which were dune sands in Mongolia millions of years ago, so that the presumption is strong that they all laid eggs.

Since the dinosaurs are supposed to have originated in a dry environment of late Permian or early Triassic time from terrestrial quadrupedal reptiles like some of the Cotylosaurs, and since the main theater of their evolution, as distinct from their adaptations, is supposed to have been in a more or less arid plains country, from which they dispersed, as adaptation permitted, to river plains, and swamps, their fossil record is much less complete than that of the mammals, for example, and their bones are found chiefly in river-flood plains and deltas and represent various end products of adaptation rather than the successive stages. Thus, in the fossil beds of western North America, their remains are absent in those late Cretaceous beds (Laramie) but are abundant in succeeding beds which some geologists regard as early Eocene.

The original dinosaur had long legs, a long tail, sharp, pointed teeth, and five toes with claws.

The dinosaurs are now divided into two main groups—the Saurischia and the Ornithischia—and some students think that the ancestors of the two were different, but this seems unlikely in spite of considerable structural differences between the two, which are probably due to modification in response to differing adaptations.

Saurischia

The name is from the two Greek words meaning "lizard-like hip joint." The Saurischia lack predentary bones in the front part of the lower jaws and have teeth in the front part of their jaws. Their toes are armed with sharp, curved claws and most of their bones are dense and hollow. Their most distinctive feature is their normal reptilian pelvis, similar to that of a crocodile, which gives them their name. A typical saurischian pelvis is shown in Fig. 136.[2] Such a pelvis is said to be triradiate—the ilium is more or less elongated parallel with the backbone, the stout pubis is simple and directed downward and forward, and the stout ischium is directed downward and backward. The

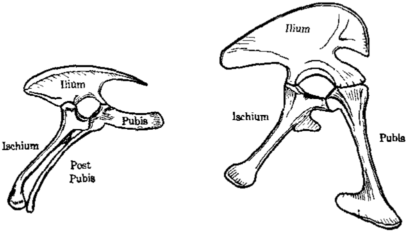

Fig. 136.—Pelvic bones of (1) Camptosaurus, one of the Ornithischian and (2) Allosaurus, one of the Saurischian dinosaurs. (*After Matthew.*)

Saurischia include the groups Cœlurosauria, Pachypodosauria, Theropoda, and Sauropoda, and among them are the earliest known forms which already were out-and-out dinosaurs, with the body raised off the ground, walking or running on their hind legs and balancing the front part of the body with the aid of the long tail.

The Cœlurosauria include at least four families of mostly small, slender, active, carnivorous dinosaurs found in the Triassic and Jurassic. Compsognathus was one of the smallest known dinosaurs. Podokœsaurus of the Connecticut Valley Triassic (Fig. 137[1]) shows the proportions of these tiny progenitors of the later Mesozoic giants. It was about 4 feet long of which about half was tail.

The Pachypodosauria were somewhat similar in appearance and habits but somewhat larger in size. They are confined

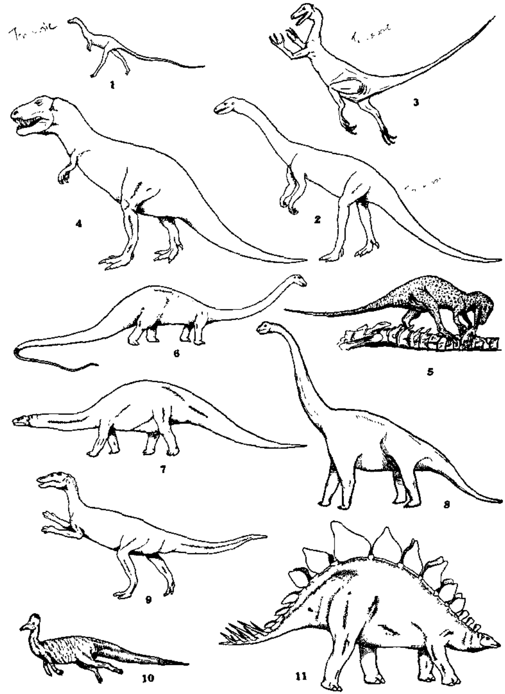

FIG. 137.—Restorations of dinosaurs. 1. Podokesaurus, one twenty-fourth life size. 2. *Anchisaurus*, one *twenty-fourth life size*. 3. *Ornitholestes*, one-eighteenth life size. (*After Knight*.) 4. Tyrannosaurus, one one-hundred-thirteenth life size. 5. Allosaurus eating the tail of Brontosaurus one one-hundred-thirty-fifth life size. (*After Knight*.) 6. Diplodocus, one two-hundredth life size. 7. Brontosaurus, one two-hundredth life size. 8. Gigantosaurus, one two-hundred-fortieth life size. (*After Matthew*.) 9. Trachodon, the duckbill, one-eighty-fifth life size. 10. Corythosaurus, the hooded duckbill, one-sixtieth life size. (*After Osborn*.) 11. Stegosaurus, one-sixtieth life size. (*Figures 1, 2, 4, 6, 7, 9, 11 are from Schuchert, after Lull*.)

to the Triassic of Europe and North America and their appearance is shown by the outline figure of Anchisaurus (Fig. 137[2]).

The Theropoda are a much more progressive group and more diversified in size and habits, ranging over the long ages from the late Jurassic to the close of the Upper Cretaceous, developing into alert, active, light-bodied forms, quite birdlike in proportions, such as was Ornitholestes of the late Jurassic of Wyoming (*Fig. 137[3]) or Ornithomimus (Struthiomimus) of the Upper* Cretaceous—still more birdlike, since it had lost its carnivorous teeth and had its toothless jaws sheathed in horn, although it is very doubtful that it had departed from the carnivorous habits of its relatives.

Allosaurus is typical of the larger-bodied theropods and is known from a very complete skeleton mounted in the American Museum of Natural History, from which the accompanying restoration was made (Fig. 137[5]). Allosaurus was 34 feet long, half of which was the balancing tail which enabled it to walk habitually on its hind legs, in which position it was about 8½ feet high. The body and head were rather compact, narrow, and deep. The mouth was large and capable of opening wide and armed with sharp, compressed, serrate-edged teeth. The feet were birdlike in structure and the toes were armed with powerful, sharp, curved claws. It was active but the small size of its brain cavity shows that it did not track its prey like a carnivorous mammal, and its huge bulk prohibited its leaping like a lion or tiger. It must, therefore, have waited for its prey and then rushed it. It may have lived largely or partly on carrion. The tooth marks on the giant vertebræ of Brontosaurus, found fossil with it, fit its teeth and were the basis for the restoration. Allosaurus has been found, also, in Colorado and in the early Lower Cretaceous of Maryland. This race of carnivorous dinosaurs reached its culmination in a form discovered in the Upper Cretaceous of Montana and named by Professor Osborn "king of the tyrant saurians," *Tyrannosaurus rex*.

Tyrannosaurus reached a length of 47 feet and stood 20 feet tall, or nearly twice the height of the largest African elephant (Fig. 137[4]). Its head was 4¼ feet long, 3¼ feet deep, and 2 feet 9 inches wide, and the powerful jaws were armed with pointed, sharp-edged teeth 3 to 6 inches in length. The massive hind legs with great sharp claws 6 or 8 inches long supported the whole weight of the body estimated to have been several tons. The

forelimbs were relatively very small and adapted for grasping. Compared with Allosaurus, this later form was of more massive proportions with more powerful jaws. Of course, its bulk precluded quick, agile movements as did also its intelligence, for the brain is estimated to have weighed only a pound. It was adapted for preying on the hugh, sluggish, horned, and armored dinosaurs. Although we can picture it in imagination, it would be worth a fortune to have been able to see Tyrannosaurus make a rush at a Triceratops.

These hugh, carnivorous dinosaurs have also been found in other parts of the world and are sometimes collectively called "megalosaurians."

The Sauropoda were herbivorous dinosaurs, mostly quadrepedal but derived from small bipedal forms like Plateosaurus of the German Triassic. Toward the close of the Jurassic and the dawn of the Lower Cretaceous they attained the largest size ever reached by any terrestrial animal. Their ancestors are later in appearing on the scene than the carnivorous dinosaurs by about a third of the Triassic period.

As speed is unnecessary in vegetarians and is, indeed, unattainable with any great increase in size, the sauropods grew to such huge proportions that many of the foremost students believe that they could move with difficulty on the land and must have spent most of their time partly submerged and feeding on aquatic plants. This conclusion is based, in part, on the massiveness of the limb, rib, and tail bones and the lightness of the back, neck, and skull bones.

Despite their great bulk and tiny brains, they became widely dispersed throughout the world in North and South America, Europe, Africa, and probably in Asia as well.

Not all of them were titans. Pleurocœlus of the Lower Cretaceous of Maryland was only 12 to 15 feet in length. The skeleton of Brontosaurus (Fig. 137^{7}) in the American Museum of Natural History is 67 feet long and in life the animal has been estimated to have weighed 38 tons. The skeleton of Diplodocus (Fig. 137^{8}) in the Carnegie Museum is 87 feet long, and Gigantosaurus (Fig. 137^{8}) from East Africa is supposed to have been still larger. All were massive and slab sided and much of the length is made up of neck and tail, especially in Diplodocus, which was the most slender of the three mentioned.

ORNITHISCHIA

Their name is derived from the Greek words meaning "birdlike hip joint." They are contrasted with the Saurischia in having predentary bones and in having the teeth restricted to the hinder part of the jaws and a horny, beaklike sheath in front. The limb bones are less dense and are armed with flattened claws, sometimes hooflike. The pelvis, as their name indicates, is more like that of a bird and may be illustrated by that of Camptosaurus (Fig. 136[1]). Such a pelvis is said to be tetraradiate. The ilium is more or less flattened and may be greatly elongated (as it is in Trachodon and Triceratops), the pubis consists of two branches—a rather stout præpubis directed forward and a slender postpubis directed downward and backward parallel with the ischium. This is very much reduced in some forms (Triceratops).

The Ornithischia, or Predentata, as they are often called, comprise the unarmored Ornithopoda or Iguanodontia, the curiously armored Stegosauria, and the horned Ceratopsia.

They all appear to have been vegetarians, early losing the teeth from the front of their jaws and developing a horny beak like that of a turtle, retaining the back teeth for grinding their food.

They appear in the later Triassic as small bipedal forms 2 to 8 feet long of which Nanosaurus from Colorado has often been regarded as the most primitive.

The Ornithopoda, or bird-footed dinosaurs, were the originals to which Richard Owen the great English comparative anatomist first applied the name "dinosaur" about the middle of the nineteenth century, basing it upon large fossil bones and footprints found in the south of England. More recently discovered material in Belgium, Africa, Asia, Canada, and the United States has given us a very perfect idea of their structure, appearance, and variations. They appear as fossils near the close of the Jurassic or at the dawn of the Lower Cretaceous and continue to the close of the Upper Cretaceous or, possibly, slightly later.

The more interesting are those later semiamphibious forms in which the front of the jaws are widened and flattened to a form like that of a duck's bill and they are consequently known as the "duckbill dinosaurs." They were exceedingly common

in late Upper Cretaceous time and a considerable number are wonderfully preserved as mummies covered with the thin, shrunken skin with traces of the muscles and tendons and nearly all the bones still articulated as in life. The front legs were small and the hands were four fingered, the first having disappeared and the fifth being considerably reduced. The hind legs were powerful and were three toed. The dorsal and ventral processes of the tail vertebræ are long, indicating a high, narrow tail and, consequently, that they had considerable swimming ability. Whether some of them spent most of their time in this amphibious mode of life or whether they took to the water to escape from Tyrannosaurus is not certain. Doubtless, at first it was an occasional safety adaptation which in some of the duckbills such as Corythosaurus (Fig. 137^{10}) became a regular habit.

Trachodon (Fig. 137^{9}) was about 25 feet long, the others somewhat smaller. Several developed ornamental modifications of the skull which took the form of a thin, high, bony crest in Corythosaurus (Fig. 137^{10}), a bony spine on top of the skull in Saurolophus, and a crested muzzle in Kritosaurus.

The Stegosauria or armored dinosaurs originated from bipedal Triassic Ornithopoda, which, during the Jurassic, became quadrupedal and heavy and developed the remarkable armor which gives them their name. Several kinds have been discovered, but the most extraordinary is Stegosaurus itself, with straight, columnar legs, hoofs on the four fingers and three toes, and an extremely small head. The brain was only about one-fiftieth the size of that of an elephant, emphasizing the stupidity of these ungainly reptilian brutes. The skin developed numerous small, bony nodules in it, and along the crest of the back there was a double row of triangular bony plates, those over the thighs being over 2 feet high and 4 inches thick at the base. The tail was armed with four or more pairs of stout, sharp spines 2 feet long and 5 or 6 inches thick at the base. Perhaps, rivals backed at each other and lashed with their spined tails. This elaborate defensive armor seems, however, to have been ineffectual, for the stegosaurs barely survived into the Cretaceous.

A restoration of Stegosaurus is shown in Fig. $137.^{11}$

The Ceratopsia, or "horned dinosaurs," for that is the meaning of their name, are the late flower of evolution among the herbivorous dinosaurs, not appearing in the geological record until

the middle of the Upper Cretaceous or, perhaps, slightly earlier in Mongolia, rapidly evolving into a variety of large, curiously horned forms, and ending their careers at the close of this period or shortly thereafter. So far as now known, they were limited to North America except for a very small primitive form from Mongolia, of which only the skull has been discovered. This, called Protoceratops, was a small, predentate animal with a triangular skull, large orbits, and no horns. One of the least specialized of North American forms is one from the middle of the Upper Cretaceous christened Brachyceratops and which may be an immature animal (restoration, Fig. 138[2]). It was a

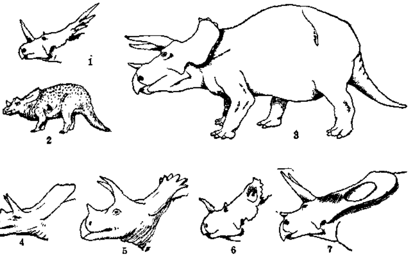

FIG. 138.—Restorations of Ceratopsian dinosaurs. 1. Styracosaurus. (*After Lull*) 2. Brachyceratops. (*After Gilmore.*) 3. Triceratops. (*After Lull.*) 4. Ceratops. (*After Matthew.*) 5. Anchiceratops. (*After Matthew.*) 6. Monoclonius. (*After Lull.*) 7. Torosaurus. (*After Lull.*) All about one-sixtieth life size.

small animal compared with the later forms and only about 6 feet long. The nasal horn core was larger than those above the eyes, and the bony frill, so characteristic of all of the Ceratopsia except Protoceratops, was not greatly developed.

The best known of the later forms is Triceratops, (Fig. 138[3]), the three-horned dinosaur, of which several different species have been found. They occur near the boundary between the Upper Cretaceous and Eocene. Their bulky build suggests no familiar animal so much as it does a rhinoceros, but Triceratops was larger than the largest rhinoceroses, sometimes reaching a length of over 20 feet, but with very short, stocky legs and a short, stout tail. Of this length, part was tail and one-fourth to one-third was the enormous head. The other groups of dinosaurs

had relatively small heads. This head is correlated with the other features of the animal and is a clear case of modification by adaptation. As the ancestral stock developed larger and larger horns for purposes of offense and defense—one horn on the nose and a pair of horns over the eyes—the roof of the skull expanded for their accomodation and support. But it was the growth backward and sidewise that added so much to its size. This was at first in response to the necessity of developing attachments for the increasing neck muscles which manipulated the horned head, but as it grew backward like a shelf it afforded protection for that most vulnerable part of the animal—the neck—so that this "frill," as it is called, went on increasing in size until it covered the back and sides of the neck and sometimes had its border armed with crests or spines.

That this was its ultimate use is shown by fossil specimens showing the scars of healed wounds and fractured and punctured edges, whether received in combats between rival males or due to onslaughts of Tyrannosaurus cannot be determined. The body proper was short and stout. There was a single row of broad teeth in the back of the mouth for grinding the vegetable food, and in front was the sharp-edged horny beak, formidably developed in some species.

Torosaurus (Fig. 138[7]), a contemporary of Triceratops, was even larger, and skulls have been found that are over 8 feet long. Within this gigantic, massive skull was a brain no bigger than that of a small dog, so that these beasts must have been excessively stupid; they probably were also slow of motion as well as slow witted and operated their bulky armament by instinctive reflexes.

Horn cores of Triceratops have been found nearly 3 feet long and the smaller are not unlike a bison horn in appearance. In life, these bony cores were covered with a horny sheath as in cattle and this must have increased their length several inches. There is considerable variation among the various genera and species in the proportions of the horns and the character of the bony neck frill, and in one genus (Diceratops) the nasal horn had become reduced to a vestige and was practically absent. Many of the earlier forms (Styracosaurus, Fig. 138[1]; Brachyceratops, Fig. 138[2]; Monoclonius, Fig. 138[6]) have the nasal much larger than the paired horns over the eyes, but in the equally early Ceratops (Fig. 138[4]) the nasal horn is much smaller than

the frontal horns, and this appears to have been the case in all of the later forms.

The bony frill had two holes in the earlier forms and in some of the later ones (Torosaurus). In others it was entire. Its edges were smooth or variously spined.

The horned dinosaurs were evidently a numerous and varied race, even though they were a relatively short-lived one. Although a few of them are rather completely known, there were doubtless many that are still locked in the rocks awaiting the explorer's pick, and it is difficult to believe that the other continents will not yield their quota of fossils to fill out the ceratopsian tree of life.

AVES (BIRDS)

The birds of the present, because of their familiarity, beauty of song or plumage, and utility as food or game, always have appealed to a wider circle than any other group of animals. Because of their power of flight they are both less retiring and more obvious than the smaller mammals or reptiles, and every small boy becomes familiar with their appearance, nests, and eggs.

Birds have been called "glorified reptiles" and they certainly have many features in common with the reptiles from which they undoubtedly took their origin. Although all authorities agree that birds and reptiles are alike in most of their structural features and that the remote ancestors of birds were lizard-like reptiles covered with scales, there is no general agreement as to precisely what their ancestors were like during the period when the scales were changing into feathers and their possessors were learning to fly. (There is no difficulty in supposing that a ribbed or keeled scale such as is characteristic of certain living reptiles could readily be modified by selection into a feather.)

It was formerly supposed that birds had been derived from small bipedal dinosaurs, but the skeletal resemblances between the two are now believed to be somewhat similar adaptations from some older common ancestry, such, for example, as the rather widely distributed Triassic reptiles of the group known as the Pseudosuchia. There is an old proverb to the effect that "A bird is known by its feathers" and the possession of feathers remains an outstanding and exclusive feature of this class of vertebrates. The chambers of the heart are completely

separated in the existing members of the class. They are warm blooded and lay eggs. The head articulates with the spinal column by a single occipital condyle (as in reptiles) instead of by two (as in amphibians and mammals). The forelimbs are modified into wings and the distal bones (tarsals and metapodals) of both the fore- and hind limbs are more or less fused. The fifth toe of the hind foot was evidently lost during their reptilian ancestry.

The skeleton in modern birds is remarkable for its lightness and strength. The walls of the bones are thin but dense and in many flying birds the marrow cavities become air cavities. About 12,000 existing species are known from all lands and their very imperfectly known geological history extends from the late Jurassic to the present.

A detailed knowledge of the skeleton is necessary for students who would study fossil birds but its description is out of place in an introductory text and the reader can understand most of the evolutionary trends among the birds, except as regards the skull, by paying some attention to the fowls that come onto the dining table, particularly the bones of the breast, wings, so-called "back" (pelvis), and legs. A mounted skeleton—that of a chicken is admirable—would, of course, be still more illuminating.

Birds are said to constitute the most uniform and homogeneous class of vertebrates but if even the little we know of their ancestral history is taken into account they are by no means so uniform as has been supposed.

Some of the outstanding modifications which the bird skeleton has undergone are (1) the consolidation of the pelvic bones, together with a greater or lesser number of associated vertebræ brought about by the necessity for increased rigidity in two-legged animals in which the hind limbs are used variously for perching, running, swimming, etc. (2) The shortening of the tail. The oldest known fossil bird had a tail longer than its body. The modern bird has less than half as many caudal vertebræ and several at the end (six or seven) are consolidated into the plowshare bone (pygostyle) which is a base for the tail feathers (rectrices) which are arranged fan wise and open and shut like a fan. (3) The lower leg bones are consolidated. (4) The forelimbs are modified into wings by consolidation of some of the bones and the loss of others, particularly some of the toes. (5) The breastbone becomes enlarged and, in flying birds, develops

a prominent keel for the attachment of the wing muscles, and there is a modification of the shoulder girdle (coracoid, scapula, and clavicle) admirably adapted for the mechanical stresses imposed on the bony framework during flight. These are but a few of the more obvious changes brought about in the skeleton, and there are similar changes in the soft parts.

Bird bones are rare fossils, infinitely rarer than the bones of any other class of vertebrates. Their general fragility helps to account for this but does not satisfactorily explain it; no more does the fact that the dead bodies might float longer before sinking and, hence, rot or weather to a greater degree or be more completely consumed by scavengers. Nor does the fact that many animals prey on birds and consume dead birds alter the fact that birds are so seldom found fossil. This cannot be attributed to their scarcity in the past, since the two earliest specimens of birds—reptile birds of the late Jurassic—belong to different species and possibly to different genera, and this is clear evidence that there must have been an unknown variety even at that early date in bird history.

Because the fragmentary bird bones that have been found fossil have usually been identified by paleontologists as belonging to living genera, it has been quite generally assumed that there has been but slight evolutionary change among birds from the dawn of the Tertiary period, but this is an unwarranted assumption and it seems probable if we ever get a more complete geological record for this time that birds will show quite as much relative progress as the mammals.

Since the geological record is so very incomplete, only a few of the more spectacular fossil birds will be mentioned, the remains of which are rather thoroughly known. The oldest and most spectacular of these is the reptile bird Archæopteryx of the late Jurassic lithographic stone found near Solnhofen in Bavaria. Its uniqueness may be indicated by the fact that it alone constitutes a subclass (Archæornithes) while all other known birds are grouped in a second subclass (Neornithes). A single feather found in 1860 was named by H. von Meyer, and shortly afterward (1861) a fairly complete individual was discovered and acquired by the British Museum. The enormous price that was paid for this specimen stimulated the quarrymen to a sustained interest in fossils, and in 1877 a second and better preserved specimen was discovered near Eichstädt and is now in the

Berlin Museum. Owen, who described the British Museum specimen, called it *Archæopteryx macroura*; Dames, who described the Berlin Museum specimen, called it *Archæopteryx siemensi*, while the original feather described by Von Meyer had already received the name of *Archæpteryx lithographica*.

The two individuals supplement one another in structural details and undoubtedly represent different species. They constitute one of the few great landmarks in avian paleontology, since no other known form shows so many reptilian features.

Archæopteryx, or the lizard-tailed bird, was about the size of a modern crow. The head was small and flat, with very large eyes, and no body feathers are known except on the back and nape. There was no beak, and both jaws were armed with small, sharp teeth set in grooves. The nostrils were well forward and the body was long and narrow. The vertebræ were biconvex and about 50 in number, of which only 10 or 11 are regarded as cervical (the lowest number of cervicals in any modern bird is 13). Instead of the few caudal vertebræ of modern birds terminated by a pygostyle for the support of the digitately arranged tail feathers, *Archaeopteryx* had a tail longer than the rest of the body and consisting of about 21 elongated tail vertebræ, each of which appears to have supported a pair of tail feathers or rectrices whose arrangement may be said to have been pinnate as opposed to the palmate arrangement of all other known birds. In the embryos of some existing birds, the caudal feathers are the first to develop and the tail is relatively elongated and is said to show a pair of feather sacs for each vertebra. The hind legs were slender, wide apart, and far back in position but were otherwise much as in modern perching birds, except that the tibia and fibula were distinct, as in most reptiles. The wings were short and rounded with three separate, sharply clawed and functional fingers. The wings carried rather large flight feathers, of which six or seven pairs appear to have been primaries and ten secondaries, and there was at least one row of wing coverts. The three pelvic bones are perfectly distinct, as in most reptiles, and, similarly, the ribs lack the hooklike processes characteristic of modern birds.

The fine-grained mud has preserved the feathers of the tail and wings with remarkable fidelity, traces of an incipient ruff at the base of the neck, and rather conspicuous quill feathers on the legs. No traces of body or contour feathers have been

discerned, so that many have concluded that the body was naked or was covered with down or tiny feathers not resistant enough to be preserved.

There has been much speculation regarding the true nature and habits of Archæopteryx and several restorations have been attempted. Most of these, although more or less realistic, are entirely too birdlike, often too heavily supplied with contour feathers, with a too massive tail. In one of these the birds are depicted as tearing at a cycad cone, although they were undoubtedly carnivorous, as their teeth clearly indicate, and they were probably fish eaters. From the position and slenderness of the legs Beddard supposed that Archæopteryx must have stood on all fours when on the ground, but this is negatived by the distinctly perching feet. Others have held that the absence of observable openings for the admission of air into the bones proved that Archæopteryx could fly only feebly if at all, but even such good modern flyers as swallows have practically non-pneumatic bones, and, moreover, we know that Archæopteryx resorted to the mud flats in search of food and, hence, must have flown from the mainland where it habitually dwelt. Finally, the well-developed feathering of the wings settles the question of flight beyond reasonable doubt. The labor of sustained flight with such short, rounded wings may, however, have been compensated for by gliding, for which the wings and the quilled legs and distichous tail were admirably constructed, and which historically must have preceded true flight.

There have been two main theories with respect to the origin of flight—the one supposing that it originated in a running, jumping ancestor and the other that it began in a climbing animal which glided or parachuted from heights as does the so-called "flying squirrel." Besides birds, true flight has been attained in certain reptiles (pterodactyls) and in certain mammals (bats) and it undoubtedly originated as a modification or amplification of the volplaning habit just mentioned.

A comparison—rather remote, it is true—is suggested between the flight of Archæopteryx and that of the modern tinamous of South America which have somewhat similar short, rounded wings. As described by W. H. Hudson, the tinamous fly violently for a maximum distance of, perhaps, a mile, but usually a much lesser distance, and then glide to the ground, repeating this two or three times before becoming exhausted. The tinamous are

ground dwellers and rapid runners, while Archæopteryx was on the other hand, clearly a partially arboreal climbing form and scarcely a runner. Its functional clawed fingers must have been

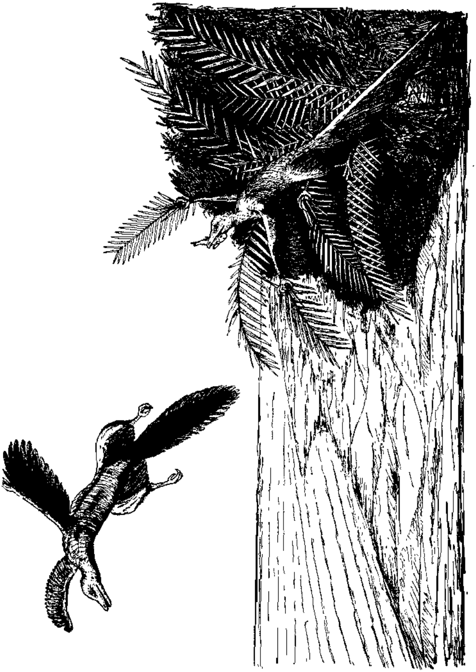

FIG. 139.—Restoration of the Jurassic reptile bird Archæopteryx.

habitually used in climbing about in the branches, much as a young hoactzin of South America climbs, and they were also useful in effecting a safe landing in flying from one tree to another or at the end of a glide.

While Archæopteryx may be considered as about 25 per cent reptilian, it is indubitably a true bird and a long way removed from its scale-covered and cold-blooded reptilian ancestors. There were bipedal, birdlike reptiles already present before the close of the Triassic, so that there were some millions of years before the late Jurassic in which to evolve feathers and acquire the art of flying, and we know that the pterodactyls had successfully solved the problem of flight by another method in that same interval.

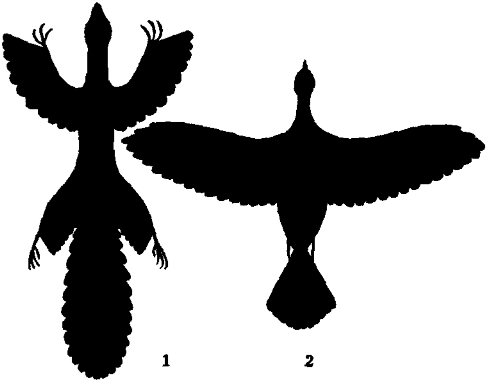

FIG. 140.—Flying outline of (1) Archæopteryx and (2) a modern bird.

The present restoration (Fig. 139), which is believed to be far more accurate as to environment and detail than any heretofore attempted, shows the strand of the Upper Jurassic mainland with the beach ridges covered with low jungle, made up largely of a mixed stand of cycads, with a few tall, leathery, fronded ferns, together with a scattering of taller conifers. In the foreground an Archæopteryx is flying. Note the slender body, the short, heavily flapped wings, the pelvic plane made by the widely spaced hind legs with their quill feathers, and the long, distichously feathered tail constituting a second plane. At the right, another Archæopteryx is shown with a small fish in its sharply toothed, beakless jaws. It is perched on the crown of a cycad

Note the long tail, the free-clawed fingers of the forelimbs firmly grasping the cycad fronds and helping to sustain the long body. The great departure in the proportions of Archæopteryx as compared with a modern bird is shown in Fig. 140. Note particularly the bill, shortened, more inflated body, larger wings, and fan-shaped tail as well as the different position of the legs of the modern bird.

The next great landmark in bird history carries us several millions of years nearer to the present and to the plains of Kansas, where, in a yellowish, impure limestone of early Upper Cretaceous age, known as the "Niobrara formation," a remarkable series of bird bones has been discovered.

The two best-known types from these deposits are quite unlike one another and are highly specialized in different directions although retaining, in each case, some very primitive features, indicating, as did Archæopteryx, that there must have been a large variety of birds in existence during the later Mesozoic from which they traced their ancestry, even though these have not yet been found fossil.

These two Upper Cretaceous types are termed Ichthyornis and Hesperornis. They are alike in the single feature that the jaws were armed with numerous small, conical teeth. Ichthyornis (Fig. 141[2]), the smaller of the two, gets its name from the two Greek words meaning "fish bird" and was suggested by the fish-like vertebræ, which are concave at both ends, as in the fishes, amphibians, and many (especially extinct) reptiles and in the early embryonic stages of modern birds. (All modern birds have saddle-shaped vertebræ.) Several species of Ichthyornis are known. They were small birds about the size of a large pigeon with powerful wings and normal bird legs, showing the main modifications, especially in the wings, which characterize modern birds, as, for example, the reduction of the digits and the coossification of the metacarpal bones. With these modernly specialized wings there was the correspondingly specialized shoulder girdle and deeply keeled breastbone (sternum), as in existing birds of strong flying powers.

Although the parts mentioned are highly specialized, we find that the large head had a small brain case with a reptilian-shaped brain (long, with prominent optic and olfactory lobes); the quadrate bone, which articulates the lower jaw to the skull, had a single head; the lower jaws were not coossified in front as they

are in all existing birds (this coossification is rather late in modern pelicans and curlews); and the jaws were armed with sharp, recurved teeth in sockets, as in many reptiles.

The position of Ichthyornis in the evolutionary tree of birds is much disputed and all that can be said is that it shows various skeletal modifications similar to those of modern strong flying birds, while retaining many primitive characters, and although it was obviously a fish-catching sea bird like a modern tern or gull, it can hardly find its place in any of the orders based on existing birds.

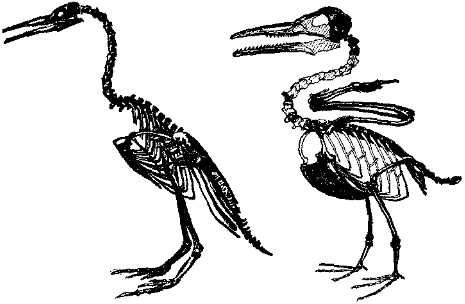

FIG. 141.—Skeletons of Upper Cretaceous toothed birds. (*After Marsh*). 1. *Hesperornis regalis*, one-sixteenth life size. 2. *Ichthyornis victor*, one-fourth life size.

HESPERORNIS

This bird is remarkable for the degree of specialization or adaptation to a swimming and diving life which is shown by its skeleton. The adaptation is eloquent of a whole lost chapter in bird evolution, for in no sense can Hesperornis be considered as reptilian and primitive, as its describer Marsh supposed.

Hesperornis was a large bird, 4 or 5 feet long, and several species, some of which are represented by nearly complete skeletons as well as impressions of the feathers, have been discovered.

The skull was relatively small, long, and narrow, with a small, long, and essentially reptilian brain. The jaws were long and

slender and were armed with numerous recurved, pointed teeth set in grooves and reptilian in structure and succession, developed on the hinder half of the upper jaw (maxillary) and throughout the whole length of the lower jaw. The mandibles were united by a ligament and not coossified, a feature unknown in the adults of existing birds. The neck was long and slender with 17 saddle-shaped cervical vertebræ—a specialized feature indicating great flexibility. The whole shoulder girdle was reduced, with the clavicles (wishbone) separate, the sternum flat and without a keel, and all of the wing bones except one—the humerus—gone. The pelvis was long and narrow (compressed) with the hind ends of the ilium, ischium, and pubis ununited. There were 12 or 13 free tail (caudal) vertebræ, the last 7 or 8 with long, flat, transverse processes and so interlocked and united that motion was possible only in a vertical direction—a remarkable diving adaptation. The legs were very long, attached near the middle of the body, which was narrow back of the hips. The articular surfaces of the leg bones show that the lower leg and foot must have stood out nearly at right angles to the body, like a pair of oars, instead of being beneath and in line with the body as in modern swimming birds, and the four partially webbed toes, of which the outer was the longest, were so attached that they turned edgewise when the feet were brought forward for the next swimming stroke, as one reduces the resistance of the water by feathering the oars in rowing.

Dollo (1881) characterized Hesperornis as a "carnivorous aquatic ostrich" and this seems to have been the conception of Marsh, its discoverer. Lucas (1922) portrays them as an "overgrown, wingless loon" but they are not related to either of these modern birds, although their swimming and diving adaptations are much like those of modern loons (Colymbus) and grebes (Podicipes), both of which are birds with well-developed wings and, therefore, could not be descended from a form like Hesperornis which had lost its wings through long-continued disuse. Many modern swimming birds use their wings under water, and in the penguins the wings are, in reality, paddles and useless for flight but enable their possessors to steer and turn around in the water with surprising agility. The ancestors of Hesperornis were too bulky and had too large wings to be strong enough for swimming in such a dense medium as water. Hence, when swimming, they were held tight against the body and gradually

dwindled through long-continued disuse at the same time that the muscles and bones of the legs were increasing in size and efficiency by constant use.

The plumage of Hesperornis was soft and smooth, of hairlike feathers, something like that of the modern snakebird (Anhinga). Judging by the skeletal features enumerated, Hesperornis was a thoroughly aquatic bird capable of rapid progress through the water and, by reason of its speed, flexuous neck, and long, slender jaws armed with recurved, sharp teeth, a proficient catcher of fish.

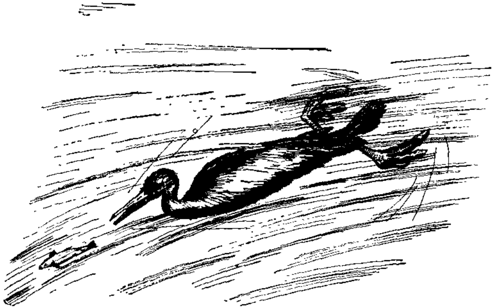

Fig. 142.—Restoration of Hesperornis. (*After Gleeson.*)

The skeleton, mounted in normal bird fashion like that shown in Fig. 141,[1] gives an altogether wrong impression, which is corrected by the restoration showing Hesperornis in its normal swimming attitude (Fig. 142). It must have been exceedingly clumsy on land but it necessarily resorted to the shore to nest and probably passed its nights on land as do our modern fishing birds. The mausoleum of Hesperornis and the contemporaneous flying reptiles (Pteranodon) is hundreds of miles from the shores of the Niobrara Sea, but there must have been islands in the near vicinity, since neither type could have traversed such great distances, and the character of the plumage of Hesperornis, easily wetted, seems to demand that it be dried daily, just as this is necessary in the case of the snakebird with which I have compared it.

Fragments of other types of Upper Cretaceous toothed birds have also been found in both North America and Europe (Enaliornis, for example), but except in the cases of Ichthyornis and Hesperornis they are very incompletely known. The diverse structural adaptations of these two preclude considering either as in the direct evolutionary line of modern groups, as has so frequently been done, but rather they give us a welcome picture of two of what must have been a large assemblage of diverse ancient birds and serve rather to emphasize our ignorance of early avian evolution.

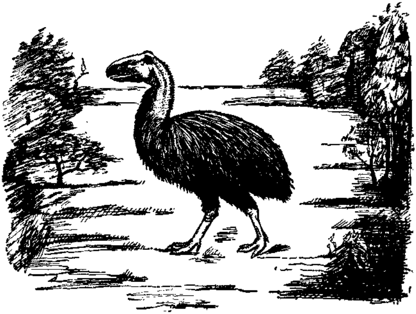

FIG. 143.—Restoration of Diatryma, about one-fiftieth life size. (*After Christman.*)

The next scene in the geological panorama of the birds is in Wyoming in Lower Eocene times and introduces the giant ground-dwelling bird Diatryma, exasperatingly specialized, so that again we get much interesting information about adaptation to a particular mode of life but little information of the course of evolution of the birds. The accompanying restoration (Fig. 143), copied from Christman, gives an accurate portrayal of Diatryma, for a nearly complete skeleton and fragments of the plumage bave been found fossil.

Diatryma comes from the Wasatch formation and was a veritable giant, standing some 7 feet tall, thus not so tall as a large ostrich but bulkier than any living bird. It is the first bird considered that surely belongs to the same subclass as the

majority of our existing birds (Euornithes or Neognathæ). As a bird especially adapted both in size and structure for running instead of flying, its wings through generations of disuse had become vestigial.

Its most remarkable feature is the extraordinary proportions of the head and beak, and this gives it a purely superficial resemblance to the giant Patagonian fossil bird which will be considered next. The head is 17 inches long and of this the beak is 9 inches long and 6 inches high; the nostrils are small; the lower jaw is rather stout; and this enormous head was borne on a short and massive neck. The shoulder girdle has been compared with that of the modern cassowaries, and the wing bones are very greatly reduced so that there probably was no external wing. The leg bones were large and massive, the femur being 15 inches long and the tibia nearly 2 feet long. The feathers are long and hairlike as in so many flightless ground birds.

Traces of three species have been found in the western Eocene and a fourth somewhat doubtful one in New Jersey, and there were similar large, flightless birds represented by imperfect material in the Eocene of Europe.

The running habits and bodily proportions of Diatryma naturally gave it a superficial resemblance to the Miocene Phororhachos of Patagonia, the Pleistocene Genyornis of Australia, and the existing emus and cassowaries of Australia and New Guinea; it is not, however, related to any of these but constitutes a distinct family which shows some affinities with Cariama or Seriema of the South American campos and is related to the familiar existing cranes (order Gruiformes).

The next character that appears on the avian geological stage is also a giant and comes from the sparsely wooded Miocene plains of Patagonia. The first finder of a fragment of a lower jaw of this feathered giant thought that it belonged to one of the giant ground sloths of that region and christened it Phororhacos, by which uncouth name it must be called (Fig. 144).

Phororhacos was another enormous flightless ground bird but not much of an habitual runner, if we may judge by its sharply clawed feet and relatively slender legs. Doubtless, its horselike neck and enormous meat-cleaver curved beak enabled it to cope effectually with its enemies, so that the lack of need for running away from enemies and the abundance of prey rendered speed a minor consideration. Despite the size of this

bird, which was 7 or 8 feet tall, the ponderous head seems out of all proportion to the body. The skull is 23 inches long and 7 inches high, or larger than that of most horses (see Fig. 145). The jaws are very narrow, the upper jaw being high and terminating in a sharp hook, and as the head was borne on a massive neck, it must have constituted a formidable weapon. The wing bones are all present but were much reduced in size so that although there was a fantastically small external wing it was

FIG. 144.—Restoration of Phororhacos, about one-fortieth life size. (*After Knight.*)

entirely functionless as far as flying is concerned. The pelvis was long and narrow and thoroughly consolidated and the legs were long and relatively slender. No trace of the plumage has been found fossil but in the restoration Phororhacos is depicted with the simple, hairlike feathers that characterize the known large flightless birds. The relationships of this bird, which is represented by a number of species in the Santa Cruz formation, is puzzling, chiefly because of its extreme modifications and the lack of complete skeletons. Naturalists tend to compare all giant ground birds with one another and with the familiar ostrich

tribe, but Phororhacos is not related to the ostriches or their allies, appearing rather to be remotely related to the modern herons, although belonging in a separate order.

The development of flightlessness and great size frequently go together and are primarily due to the absence of enemies. Thus, among existing flightless birds, the ostrich inhabits the deserts of Arabia and Africa; the rhea, the arid country of northeastern Brazil and Patagonia; the emu, the Australian arid plains, the cassowaries, the scarcely habitable thickly wooded islands of Malaysia. These are all moderately large, the ostrich being the largest living bird. The singular Apteryx of New Zealand is a

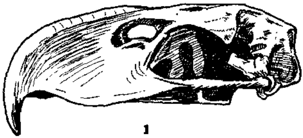
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FIG. 145.—The skull of Phororhacos (1), compared with that of a modern horse (2). (*After Lucas.*)

small bird, nocturnal in habit, and the host of penguins of the southern hemisphere offset their lack of flight by their superb submarine ability. Isolation is, then, the likeliest situation where enemies are fewest, and, hence, islands are the regions where flightless birds have been commonest and where in the past they have reached the largest size. With the growth of trade and intercourse these have either become wholly extinct like the dodo of Mauritius or the solitarie of Rodriguez, or nearly so like the Apteryx of New Zealand.

The most remarkable examples of giant island birds are the moas of New Zealand and the Æpyornis of Madagascar, which are worthy of some description, even though this has often been attempted.

In New Zealand the bones of moas are scattered over hill and dale, they have been found in caves and dug out of swamps. In draining a small pond near Canterbury over 2,500 bones representing no less than 800 individuals were found. Over 20 different species have been discovered, ranging in size from that of a turkey to that Goliath of moas, *Dinornis maximus*, which was 10 feet or more tall, thus much larger than the biggest ostrich and the largest known bird (Fig. 146). The smaller species were

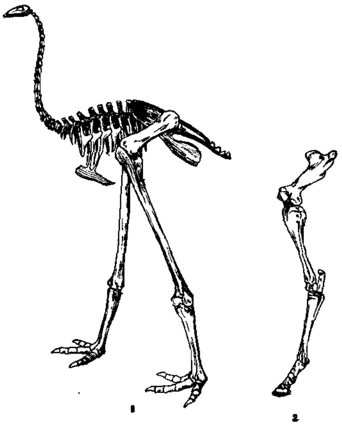

FIG. 146.—Skeleton of Dinornis maximus (1) compared with the leg bones of a modern horse (2). Both about one-fortieth life size. (*After Lucas.*)

naturally the more common. The head is small; the neck long and massive; they had been flightless for so long that the wing bones had entirely disappeared; even the shoulder girdle was vestigial.

What they lacked in wings they made up in legs, for the legs of the largest is one-third longer than that of a good-sized horse and the drumstick (tibia) is 39 inches long, or more than twice that of an ostrich and seven times that of a turkey. The abundance of moa bones indicates that they were on the wane in the late Pleistocene, possibly because of the inhospitality of glacial

conditions, but the aborigines in a land where meat is scarce evidently completed their extermination, for their charred bones and egg shells are found mixed with flint implements and the remains of wood fires.

The elephant birds of Madagascar (Æpyornis) were not quite so huge as the moas but are interesting because they laid the largest known eggs of all time, and it is these enormous eggs 13 inches long and 9 inches in diameter, equal to half a dozen ostrich eggs or 13 dozen hen's eggs and with a volume of over 2 gallons, which were the basis of the Arabian legends of the roc of Sindbad the Sailor.

Æpyornis bones are found chiefly in the deposits of ancient shallow lakes. There were several species—over a dozen have been described. They all had small heads, very rudimentary wings, and very massive legs. Quantities of broken egg shells and bones have been discovered, but the skeleton is less completely known than that of the moa.

MAMMALIA (MAMMALS)

Mammals may be defined as warm-blooded, air-breathing animals, more or less covered with hair. In all but the primitive Monotremata the young are produced alive (viviparous) and in all but these egg-laying monotremes, and the Marsupalia, the embryo is nourished by the mother's blood before birth through the placenta and afterward by milk secreted by the mammary glands. Hence, the familiar mammals are called "placental mammals," and the name of the class—Mammalia—is derived from the Latin *mamma* or "breast."

The skull has two articulations (occipital condyles), as in the Amphibia, and not one, as in birds and most reptiles. Each half of the lower jaw is a single bone articulating directly with the skull without the interposition of the quadrate bone such as is utilized in birds and reptiles.

The teeth, typically 44 in number—in man it is smaller, being 32—are generally differentiated (heterodont) into incisors, canines, and premolars in the first set or milk dentition. These are replaced during youth by an adult set adding back of the premolars the molars which are unrepresented in the first set. This is sharply contrasted with the indefinite succession so remarkably developed in some of the reptiles (*e.g.*, the predentate dinosaurs) where, also, there is but slight differentiation among

the individual teeth, only those reptiles known as the cynodonts approaching the mammals in this respect. Mammals are characterized by having the ankle joint between the leg bones (tibia and fibula) and the ankle bones (tarsus) and never between the tarsal bones, as in birds and reptiles. The trunk is also divided into a thorax or chest and an abdominal cavity by a muscular partition—the diaphragm. The lungs and the completely four-chambered heart are lodged in the former, and the bulk of the digestive, excretory, and reproductive organs in the latter.

The two mammalian structures which show the widest range of adaptional variation are the teeth and the feet. Vertebrate paleontologists differ as to which are more reliable as indicators of evolutionary trends and relationships. The truth is, of course, that sometimes one and sometimes the other set of characters is most important. Sometimes, great differences in dentition may occur among the members of the same family (*e.g.*, the Viverridæ), and, similarly, unrelated forms often have very similar dentition. The same features are true of the feet; elongation and reduction of the toes acquired in independent lines often follow identical adaptations. Thus, the genus Thoatherium (Litopterna) has a one-toed foot remarkably horselike, Nesodon (Toxodontia) has a foot like a rhinoceros, and hosts of similar examples might be mentioned. The truth here, as in the case of all organisms, is that no single character or set of characters is always reliable, and those parts less effected by the environment, such as the ear bones, skull foramina, brain, and reproductive organs, may give surer clues to relationships. On the other hand, the student should remember that the teeth are the parts of mammals most frequently preserved as fossils; in fact, probably the majority of fossil mammals, especially in Europe, are known chiefly from their teeth, so that the dentition occupies a predominant place in mammalian paleontology.

The structure of the teeth varies greatly. A tooth consists of a crown above the gum and one or more roots inserted in the jawbone. In special cases, as in the teeth of the armadillo and the gnawing front teeth of the rodents, these are rootless and grow throughout life to compensate for the wear. The tooth substance is of three kinds—dentine, enamel, and cement. One or the other may be absent in special instances. The cement is a form of bone tissue. In low teeth like man's it

merely forms a covering over the roots and does not appear above the gums, but in high teeth like those of modern horses and elephants the cement encases the whole tooth, filling all the depressions and irregularities.

The dentine or ivory is the indispensable tooth substance and makes up the bulk of most teeth. Its structure is unlike ordinary bony tissue. The enamel is very hard and dense and usually covers the entire crown. In special cases, it does not cover the crown but is arranged in bands so that the differential wear prevents the crown from becoming smooth and the tooth useless. This is shown most beautifully in elephants' teeth (see account under Elephants) or in the incisors of a rodent. If these are examined in a squirrel or beaver it will be seen that the enamel coats the front edges; hence, no matter how great the wear, the enamel is so much harder that the incisors always have chisel-like tips.

Primarily, teeth are for seizing and masticating food; secondarily, they serve for offense and defense. The carnivores have teeth for shearing flesh and crushing bone, the herbivores for cropping and chewing vegetation, the insectivores for catching insects, the rodents for gnawing. Hence, the characters of fossil teeth are useful not only in determining the nature of the food and the consequent habits of their owners but also for giving us clues to their bodily form, since the nature of the food has a profound influence on the proportions of the body.

The typical number of teeth for warm-blooded animals is 44, that is, 3 incisors, 1 canine, 4 premolars, and 3 molars in each half of each jaw, but most animals have this modified in various ways and usually with a smaller number than 44. Thus if the teeth are counted in a dog's mouth, 12 incisors, 4 canines 16 premolars, and 4 upper and 6 lower molars will be found, o 42 in all. If a sheep's mouth is examined, no incisors or canine will be found in the upper jaw, and the total number of teeth wi be 32. Students of teeth have a useful way of writing thes tooth formulas. Man's would be written thus: $i\,\frac{2}{2}\,c\,\frac{1}{1}\,p\,\frac{2}{2}\,m\,\frac{3}{3}$ fo one side of the mouth. The typical formula for mammals woul be written $i\,\frac{3}{3}\,c\,\frac{1}{1}\,p\,\frac{4}{4}\,m\,\frac{3}{3}$. That of the dog is $i\,\frac{3}{3}\,c\,\frac{1}{1}\,p\,\frac{4}{4}\,m\,\frac{2}{3}$; an that of the sheep is $i\,\frac{0}{3}\,c\,\frac{0}{1}\,p\,\frac{3}{3}\,m\,\frac{3}{3}$. Since these are for one si of the mouth—upper teeth above the line, and lower teeth belo the line—the total must be multiplied by two to get the comple number in the mouth.

Since the jaw fulcrum is the glenoid articulation, the front teeth *sweep through a wider arc, move more rapidly*, and are less powerful than the back teeth; the back teeth move a lesser distance and with greater force. Hence, there is always the tendency for the teeth to separate into a forward series adapted for gnawing, cropping herbage, biting, or grasping and a back series for crushing or grinding. The incisors and canines constitute the forward series and the molars are the chief constituents of the hinder series. The premolars are intermediate in position but partake in the functions of the molars, which they come to approximate in structure, whereas the front teeth depart less from the original tooth form. The modifications by means of which a primitive conical tooth becomes the incisors and canines, as we find them, involve no theoretical considerations. Paleontologists are less agreed regarding the manner of evolution of the molars.

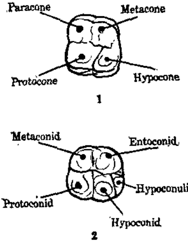

FIG. 147.—Crown pattern of upper (1) and lower (2) human molar teeth.

The crown of a typical molar tooth is not flat but has a number of elevations on it known as "cusps." The principal cusps are usually named as shown in Fig. 147.

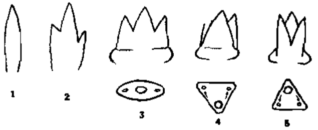

FIG. 148.—Evolution of molar teeth according to the trituburcular theory. 1. Reptilian tooth. 2. Triconid tooth as in Dromatherium of the Triassic. 3. Amphilestes of the Jurassic, side view and ground plan. 4. Inside view and ground plan of an upper tooth with rotated cusps. 5. Inside view and ground plan of a lower tooth with the cusps rotated. In the opposite direction from that in Fig. 4.

All are agreed that mammalian teeth passed through a triangular or trituburculate stage. The manner in which a typical molar was molded, however, has been variously interpreted by different students. *According to the Cope-Osborn* "tritubercular theory" (Fig. 148), the front and back cusps of the upper

teeth rotated outward and those of the lower teeth rotated inward so that the crowns were reversed triangles, the upper triangle (trigon) with its apex internal (on the tongue side), the lower triangle (trigonid) with its apex external (on the cheek side). Such a shifting may explain the evolution of the teeth in the extinct triconodonts of the Mesozoic, but it does not appear to fit for the so-called Trituberculata or the later placental mammals.

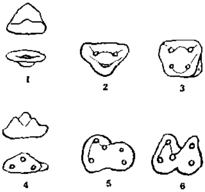

FIG. 149.—Evolution of molar teeth. (*According to Gregory.*) 1. Profile and ground plan of an upper molar as seen in the Cretaceous mammals from Mongolia. 2, 3. Ground plans of later stages. 4. Profile and ground plan of a lower molar in the same stage of modification. 5, 6. Ground plans of later stages.

In these, according to Gregory (Fig. 149), there has been *no shifting* of cusps, but the upper and lower molars early assumed somewhat different forms, the original cusps remaining on the outer or cheek side. The front inner cusp was not the shifted first cusp of the ancestral tooth but a new growth from the enlarged base. The recent finding of Cretaceous mammal skulls in Mongolia supplies such a missing evolutionary link in which the upper molar has not yet separated into two cusps and there is a heel on the inner side foreshadowing the so-called "protocone," while in the lower molar there are three cusps arranged in a triangle with a heel on the back. This heel develops and widens in the later mammals as shown diagrammatically in Fig. 149.

Limbs.—The limbs of all of the vertebrates other than fishe or those mammals (whale, seal) and reptiles (ichthyosaur, snake in which they have become much modified consist of the le and foot (arm and hand). The fundamental ground plan of limb (Fig. 150) comprises a single long bone (humerus or femu which articulates with the limb girdle of the trunk, followed b two long bones side by side (radius and ulna, tibia and fibula At their distal end is the ankle (tarsus) or wrist (carpus) consis ing of a number of small bones, followed by five metacarpal metatarsal bones forming the bases of the five digits (fingers toes) which are made up of phalanges. These various lin bones are never found with straight, articular surfaces but a endlessly adapted for the mechanical functions which they pe form, according to the habits and heredity of their owners.

No part of the vertebrate skeleton affords such readily understood evolutionary series as the marvelous modifications of this simple ground plan of limb structure in the different animal groups. The bones become shortened or elongated, develop processes, modify their articular surfaces, and become variously consolidated. A flying bird or a racing horse have only to be called to mind in order to realize the terrific mechanical stresses and strains that the limbs sustain; and were not their modifications well-nigh mechanically perfect, they would utterly fail to function.

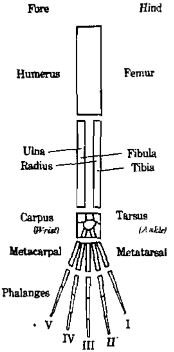

FIG. 150.

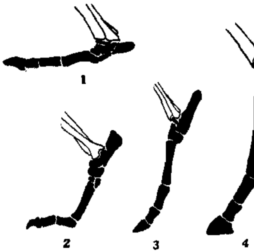

FIG. 151.

FIG. 150.—Diagram of the vertebrate limb bones. (*After Swinnerton.*)

FIG. 151.—Different types of foot adaptations. The ends of the leg bones are shown in outline, and one series of the foot bones including the nail, claw, or hoof are in solid black. 1. Plantigrade as in a bear or man, one-fifth of toe bones shown. 2. Digitigrade as in cats and dogs, one-fifth of toe bones shown. 3. Unguligrade as in the pig, showing one of the two series of functional toe bones. 4. Unguligrade as in the horse; the single series in all they have.

There will be a considerable amount to say in the proper place of the changes which these bones have undergone in certain groups. At present, it will suffice to mention the membranous wings of the bat (a mammal) supported by the greatly elongated fingers; and the leg of a cow, in which but two metacarpal or metatarsal bones remain; these are elongated and firmly united and support the third and fourth digits which bear the cloven hoof. A cow, therefore, walks on the tips of its third and fourth toes. In the horse it is the tip of the third toe upon which the animal walks. In mammals, therefore, the number of functional

toes, whether the primitive number of five, or four (hippopotamus), three (rhinoceros), two (cattle, camel), or one (horse), denotes roughly the degree of evolutionary change that has taken place in this part of the skeleton.

There are four principal and many special directions in which the feet become adapted for different habits of life. These four are fossorial for digging and burrowing habits, natatorial for swimming, cursorial for swift terrestrial movement, and arboreal (scansorial) for a life in trees. If flight were not limited to the bats, a fifth principal direction of adaptation might be added—the aerial or volant—and adaptations might be added for jumping (saltatorial), exemplified by the kangaroo, and gliding or volplaning (glissant), exemplified by the flying squirrel.

These directions of adaptation have been followed to different extents and in different ways during the long period of the age of mammals during which the orders of mammals as we know them were evolved.

The primitive mammals were small animals relatively slow of movement, something like modern insectivores, with simple, low teeth and plantigrade feet, with five toes provided with claws. The evolutionary trends comprise a general increase in size and a greater or lesser departure from generalized or general-utility structures to specialized or adapted structures. Some of these may be considered briefly:

Cursorial.—In animals which have become adapted for fast movement on the ground, the most obvious change is the lengthening of the limbs, especially the distal bones. This is accompanied by a modification and fusion of bones, as in the case of the radius and ulna where any rotation of the limb would be a hindrance to the rapid backward-and-forward movement in running or jumping. There is a change in the posture of the foot which passes from plantigrade to unguligrade and loses one to four of its digits. In these changes, the hind limbs become modified more rapidly than the forelimbs, and, generally, the neck elongates concomitantly with the limbs in order to keep the animal's mouth within reach of the ground (for food and drink). The shoulder and hip joints remain conservative because the animal must lie down and get up.

The structure of the limbs of extinct animals give us a very valuable insight into their habits. For example, in hard-ground runners, the functional digits are reduced to one (horse) or two

(antelope). Those which frequented soft ground, like the three-toed Miocene forest horse (Hypohippus) or the modern reindeer and caribou, retain the use of the side toes because of the additional support which they afford. Rapidly moving animals which have adopted jumping instead of running habits (kangaroo) have only the hind limbs lengthened and greatly modified. The front limbs become reduced and the neck becomes shortened.

Fossorial.—This term is sometimes applied to animals that live aboveground and root for food, like pigs, or dig for it, like the elephants. It is more strictly applied to true burrowers. These have their shape modified, with reduction in size of ears and sensitiveness of the eyes; the tail becomes shortened; the front limbs are shortened and strengthened for digging, and the hind limbs follow a different line of adaptation for kicking backward the dirt excavated by the forelimbs.

Natatorial.—The adoption of a partial or wholly aquatic mode of life brings about readily recognizable changes in bodily structure, dependent on the degree of adaptation and the food habits, that is, whether vegetarian or predatory. The body form becomes shaped to reduce friction, with a reduction of projecting parts and the modification of the limbs or tail, or both, for swimming.

The most complete aquatic adaptation among mammals, such as we see in a dolphin or whale, which are thoroughly fishlike in appearance, although they are viviparous and nurse their young just like their terrestrial ancestors, is a marked shortening of the brain case (cranium) and the neck, a lengthening of the jaws (face), a lightening of the bones, a change in the position of the eyes and nostrils, a loss of external ears and great structural modification of the inner ear; a partial or entire loss of hair and the substitution of a layer of fat to guard against temperature changes, since wet hair is a most ineffectual blanket. The teeth and limbs become greatly modified, the teeth becoming simplified and the limbs ultimately becoming finlike flippers, or the hind pair disappear altogether as the tail fin becomes more and more the organ of propulsion.

Scansorial.—In the climbing animals every degree of adaptation is observed according to the particular habits of the animal. Thus, many carnivores, rodents, and insectivores, although admirable climbers like the common cat, are equally at home on the ground. Those which are almost entirely or wholly

arboreal diverge in different directions, such as the so-called "branch runners" (squirrels and lemurs), those which hang from branches like the sloths, or those which swing from branch to branch by their forelimbs (brachiation), as do most of the primates.

Volant.—The only true volant mammals are the bats which have developed winglike membranes supported by the elongated digits.

The so-called "glissant" or gliding mammals which volplane through the air often accomplish wonderful flights. This adaptation is one that has arisen in many unrelated orders and involves principally the formation of skin folds to act as parachutes without great structural changes. Among the gliders are members of the marsupials (flying phalangers), rodents (flying squirrels), insectivores (Galeopithecus), and primates (the lemur, Propithecus).

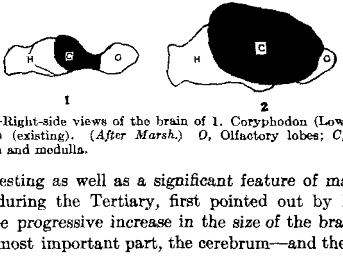

FIG. 152.—Right-side views of the brain of 1. Coryphodon (Lower Eocene). 2. Rhinoceros (existing). (*After Marsh.*) *O*, Olfactory lobes; *C*, cerebrum; *H*, cerebellum and medulla.

An interesting as well as a significant feature of mammalian evolution during the Tertiary, first pointed out by Marsh in 1874, is the progressive increase in the size of the brain—especially the most important part, the cerebrum—and the contrast in brain size and proportions, particularly between the archaic mammals of the early Tertiary and those progressive stocks which survive to the present.

No student of animal behavior would consider a modern rhinoceros so intelligent as some other ungulates—the horse, for example—but if the brain of a rhinoceros be compared with that of the Lower Eocene Coryphodon (order Amblypoda), an animal of similar size and proportions, the difference is very great, as may be seen in Fig. 152, which shows the two brains in side view. This is not the whole story, for the rhinoceros cerebrum is proportionally as much wider as it is higher than the cerebrum of Coryphodon. Although brain size is by no means the sole factor in survival, else only intelligent animals would

OUTLINE OF MAMMALIAN CLASSIFICATION

(Simplified from Scott)

- Prototheria (egg laying)
  - Protodonta (tiny Triassic forms, possibly reptilian)
  - Monotremata (Australian duckbill and its allies)
- Eutheria (*viviparous*)
  - Didelphia (*pouched*)
    - Triconodonta (Mesozoic)
    - *Marsupalia (opossums, kangaroos, etc.)*
  - *Monodelphia* (placental)
    - Unguiculata (clawed)
      - Trituberculata (Mesozoic)
      - Insectivora (moles, shrews, hedgehogs, etc.)
      - Tillodontia (Eocene)
      - Dermoptera
      - Chiroptera (bats)
      - Carnivora (beasts of prey)
        - Creodonta (early Tertiary)
        - Fissipedia (cats, bears, weasels)
        - Pinnipedia (marine carnivora, seals and walruses)
      - Rodentia (rabbits, beavers, mice) (*gnawers*)
      - Tæniodontia (Eocene)
      - Edentata (sloths, ant-eaters, and armadillos)
      - Pholidota (pangolins)
      - *Tubulidentata* (aard varks)
    - Ungulata (hoofed)
      - Condylarthra (Eocene)
      - Amblypoda (Eocene)
      - Artiodactyla (even toed)
        - Primitiva (Eocene)
        - *Suina* (*swine, hippopotamus*)
        - Tylopoda (camels and llamas)
        - Tragulina (chevrotains)
        - Pecora (deer, antelope, cattle)
      - Perissodactyla (odd toed)
        - Chelodactyla (horses, tapir, rhinoceros)
        - Ancylopoda (chalico*theres*)
      - Proboscidea (elephants)
      - Barytheria (Oligocene)
      - Embrithopoda (Oligocene)
      - Sirenia (manatees and dugongs)
      - Hyracoidea (conies)
      - Extinct South American ungulates:
        - Toxodontia
        - Astrapotheria
        - *Litopterna*
    - Cetacea (whales, dolphins, and porpoises)
      - Zeuglodontia (extinct)
      - Odontoceti (toothed whales)
      - Mystacoceti (whalebone whales)
    - Primates (with nails on their digits)
      - Lemuroidea (lemurs)
      - Anthropoidea (monkeys, apes, and man)

comprise the living fauna, it is an important one. Some of the ways in which it operates are in the defense and care of the young, in general alertness, and in adaptability to changing conditions, that is, in learning means of self-preservation, not only during seasons of adversity but also in the face of changing environments or new enemies.

The most complete and easily understood evolutionary series among the mammals are to be found among the hoofed mammals (Ungulata)—horses, tapirs, rhinoceroses, elephants, camels, etc., so that most of our illustrations will be taken from this group. The herbiverous mammals are sociable (gregarious) and live in herds. They are, therefore, more numerous and much more likely to become preserved as fossils than the solitary carnivores that preyed on them. The adaptive changes in their teeth and feet are also more obvious.

The Ungulata (Latin *ungula*, a hoof) were originally small, five-toed, plantigrade animals with small brains and teeth adapted for eating succulent vegetation, scarcely distinguishable from the contemporary clawed mammals.

During the Tertiary they evolved into 10 to 12 orders with a great many suborders, as may be seen from the outline of mammalian classification (p. 295).

The first evolutionary history to be considered is that of the camels.

Artiodactyla (the Even-toed Ungulates)

The great even-toed group of Ungulata (Artiodactyla) includes the pigs, hippopotamuses, peccaries, camels, deer, antelopes, sheep, and cattle as well as several wholly extinct groups such as the dichobunids of the Eocene; the entelodonts of the Oligocene; the anthracotheres, which became extinct in the Middle Pliocene and were, perhaps, the stock from which the hippopotamuses were derived; the Cænotheres of the Old World Upper Eocene and Oligocene; and the Oreodonts of North America which were primitive ruminants that became extinct in the Lower Pliocene.

The Artiodactyla fall naturally into two large groups—those which chew the cud, or ruminants, of which the cow is a familiar example; and those which do not chew the cud, or non-ruminants, of which the pig is a familiar example. The group chosen as an example of artiodactyl evolution is that of the camels, or suborder Tylopoda, as they are technically called.

If you were asked What is a camel? you would at once think of the single-humped dromedary (*Camelus dromedarius*) of Arabia or the two-humped bactrian camel (*Camelus bactrianus*) of central Asia—the well-known "ship of the desert" of song and story, circuses and zoological parks. These are the two existing species of the genus Camelus. They can be successfully crossed and the resulting mule camel has the single hump of the dromedary mother and the long hair of the father and is preferred to either pure breed for man's use.

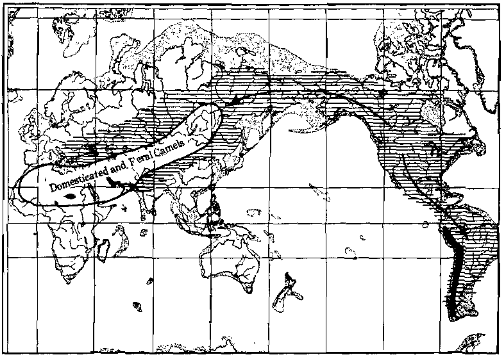

FIG. 153.—Map showing the past and present distribution of the camel family.

The area where Camelus is found is shown in Fig. 153. When Camelus was first domesticated is not known, but it was in Asia and a long time ago, so long ago that most students doubt that there are any wild camels in existence other than those that have escaped from domestication and returned to a wild life (feral). Camels were introduced into Africa in the second or third centuries, and a few were once introduced into our Arizona desert where they eventually died out. They have also been introduced into the Australian desert, where they still survive.

There is a second living genus of camels (Auchenia or Lama), also with two species—the guanaco (*Auchenia huanacus*) and the vicuña (*Auchenia vicugna*) found in the Andes Mountains of South America from the equator southward to Cape Horn,

whose domesticated representatives are the llamas and alpacas—"the sheep of the Incas."

It will be many years before automobiles or railroads will displace the camels from the caravan routes across the arid wastes of the Old World, and probably a very much longer time before the llamas will be displaced in the Andes, for they can go where a mule cannot follow and they find their own food.

No animals seem more foreign to North America than camels and llamas, and yet the family history was wholly North American until Pliocene time, when one branch of the family had reached central Asia across the Behring Straits land bridge and the other branch had reached South America. The Old World camels and the New World llamas are superficially very different in appearance—the llamas being smaller and more slender, with long ears and no humps—but their skeletons and teeth are very similar. The hump is a device of nature for storing nutriment against a time of need. It leaves no trace on the skeleton, and, hence, there is no way of telling whether a fossil form was humped or not. In general, however, the hump is considered to be a very modern adaptation, and most fossil forms are considered to have more nearly resembled the modern llamas than the modern camels.

In order to understand the evolution of the camel family, a very brief account of the end products of that evolution is necessary. In the Old World camels (genus Camelus) the skull is long, with an abruptly narrowed face, and the orbits are completely ringed with bone. The neck is extremely long, and the vertebræ show certain peculiar features. The legs and feet are very long, and both the ulna of the foreleg and the fibula of the hind leg are very greatly reduced. Each foot has but two toes (third and fourth), and the two metapodials (third and fourth) are united with one another to form a long "cannon bone," as it is called, but this cannon bone differs from similar structures in other ungulates (cattle, horses) in having the lower ends of the constituent metapodials divergent. The hoofs at the ends of the toes are hardly more than nails and do not carry the weight of the animal, which is supported by pads of elastic tissue underneath the phalanges. In the camel jaw the first and second upper incisors have disappeared, but the third incisor, the canine, and the first premolar have become like canines and have a considerable space between them. The second premolar is lost, the third and fourth are like molars but small. The lower incisors

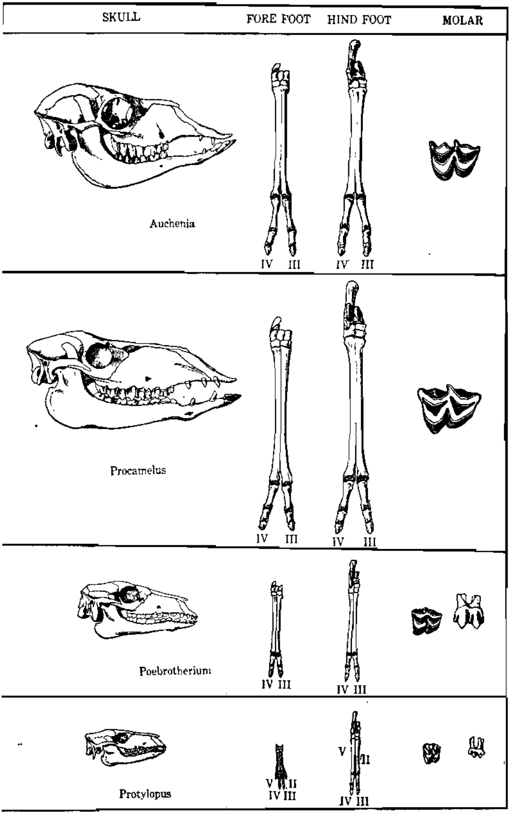

FIG. 154.—Showing the stages in the evolution of the skull, feet, and molars in the camel family. (*After Scott.*)

have all been retained and are large and shovel shaped; the canine and first premolar are pointed and spaced to work against the spaced third incisor, canine, and first premolar of the upper jaw, forming a highly efficient lacerating mechanism. There is but 1 additional premolar left in the lower jaw which is a rather small grinding tooth. The true molars, 12 in all, are large and crested (selenodont) with high crowns. The tooth formula is, hence, $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{3}{2}$, $m\,\frac{3}{3}$.

The South American llamas have a skeleton and teeth very similar to those of the Old World camels, differing merely in size and proportions and in lacking the pointed first premolar. The remaining premolars are smaller and the tooth formula is $i\,\frac{1}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{2}{2}$, $m\,\frac{3}{3}$. The cranium is relatively larger and the two toes are more distinctly separated. Llamas lack humps, have longer and more pointed ears and woollier hair—especially the alpaca—and it is these features that account for the dissimilar appearance of the two living branches of the camel family.

Special adaptations of the Old World camels for desert life are their flat, spreading feet, the water reservoirs in the walls of the stomach, the humps for storage of fat, the position of the head with eyes and nostrils on the upper side for protection against the reflected light and heat from the ground, and the nostrils capable of shutting to keep sand out, the eyes, for the same reason, having long lashes and the ears being full of hair. Their senses of sight and smell are keen, as in all desert animals, and they can scent water a long distance away. Most naturalists agree that camels, and this applies to both the Old and the New World types, are domesticated in the sense that they are too stupid to be unmanageable; in the inhospitable regions to which they are adapted they are not only beasts of burden but also sources of food, clothing, leather, etc. Both the nomads of the Old World and the Andean Indians could scarcely exist without them.

The earliest fossil form that can be certainly related to the camel line is a small animal from the Upper Eocene (Uinta formation) which has been christened Protylopus. Protylopus was about the size of a baby lamb, with hind legs considerably longer than forelegs, so that its back sloped forward. The ulnas and fibulas were entirely complete but slender. The forefeet had four functional toes, although the second and fifth were shorter than the third and fourth and evidently on their way toward

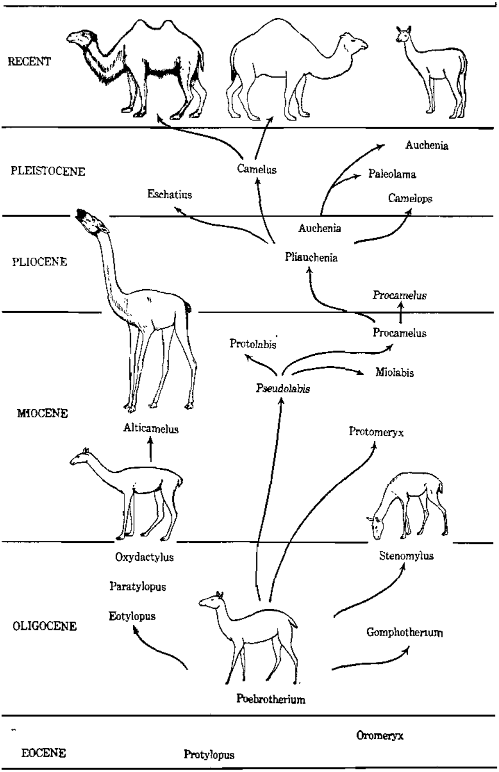

FIG. 155.—The evolution of the camel family.

disappearance. On the hind feet there were but two functional toes, but the second and fifth were still represented and their metapodials were reduced to slender splint bones, still carrying at their ends, however, vestigial toe bones (phalanges).

Thus, just as was the case in the ancestral horses, the hind feet were changing more rapidly than the forefeet. The skull of Protylopus was small, flat, and narrowed in front, with the bony orbit open behind; and all of the teeth of the primitive mammalian series were present and but slightly modified. Thus, they were in a continuous series (no spaces between them), the canines were but slightly longer than the incisors, and the molars had low crowns and four cusps. The tooth formula was $i\,\frac{3}{3}$, $c\,\frac{1}{1}$, $pm\,\frac{4}{4}$, $m\,\frac{3}{3}$.

It is not feasible to restore this ancient and tiny cameloid because no specimens have been discovered in which the neck was preserved. There is some doubt as to whether or not Protylopus is in the direct ancestral line of the camels, but its skeleton is better known than that of its contemporary of the genus Oromeryx, and it illustrates in a rather perfect manner our conception of the first stage in the evolution of camels. Scott, who has made a special study of camel evolution, thinks that the genus Homacodon of the middle Eocene (Bridger formation) and Trigonolestes of the lower Eocene (Wasatch formation) may represent the earlier ancestors of Protylopus, but both of these earlier forms are incompletely known and this surmise cannot be proved.

The evolution of the camels does not differ materially from that of the horse, except that the third and fourth toes are the ones that were enlarged and shared equally in the foot function, instead of only the third toe, as in the modern horse. This marks one of the outstanding distinctions between the odd toed (like the horse) and the even-toed (like the camel) ungulates. In both lines there was the same progressive increase in body size, the same lengthening of the legs and feet and the reduction of the side toes, a similar reduction in ulna and fibula, and heightening of the crowns of the grinding teeth.

During the Oligocene, camels were numerous, at least six or seven different genera being known, and these represent several different evolving lines of descent, due, perhaps, to the extensive replacement of forested by plains type of country in western North America at that time. One of the best-known genera, one with several Oligocene species, is Pœbrotherium.

Pœbrotherium was about the size of a sheep but of a more slender and graceful build, with a longer neck and limbs. Its slender legs and arched back gave it an extremely gazelle-like appearance. Except for the increase in size and the somewhat more advanced reduction of the side toes, it was not very different from the Eocene Protylopus. All 44 teeth were present and the main progressive tooth feature was a slight increase in the height of the lower molars. The orbits were still open behind, but the ulna had become united with the radius and the fibula had disappeared except at the two ends.

In the uppermost Oligocene or, perhaps, the Lower Miocene of Nebraska are found evidence of two other lines of cameloid evolution. One of these, represented by an abundance of fossils, is the so-called "gazelle camel," Stenomylus, a very small and delicate animal. All of the feet have but two toes, and the canines and first premolars are incisor-like. Nothing is known of the immediate ancestry of Stenomylus, nor have any descendants been discovered. A second evolutionary series is represented by the genus Oxydactylus, an early stage in a series of forms which gradually became giraffe-like in appearance and, presumably, in habits of life, and which culminated in the genus Alticamelus of the later Miocene and Lower Pliocene.

Oxydactylus, as may be seen from the restoration, was not especially giraffoid, but it was larger than its contemporaries and had a longer neck. The molars were lengthening, and the two metapodials of the foot had not united to form a cannon bone, although this had been accomplished by the time that Alticamelus appeared on the scene. Alticamelus shows many adaptations as compared with its lower Miocene forebear, Oxydactylus. It was much larger with a small head and very long neck and legs, presumably fitted for browsing upon the foliage of trees which was out of reach of its contemporaries.

The name "giraffe camel" does not imply any relationship with the true giraffes. In Alticamelus the forequarters are not higher than the hind quarters, nor are all of the neck vertebræ (cervicals) elongated as in the giraffe. The giraffe camels appear to have been peculiar to North America and became extinct with Alticamelus.

Returning now to the grazing line of camels represented by Pœbrotherium of the Oligocene, we find them represented in late Oligocene time by the incompletely known genera Gompho-

therium and Pseudolabis. During the Miocene there were several genera. The earlier of these genera (Protomeryx, Protolabis, and Miolabis) still retained a full set of 44 teeth, but the molars had become higher crowned than in the earlier forms. In most of these early Miocene species the metapodials had not yet fused to form cannon bones, and although the feet were two toed, they were still more deerlike than camel-like.

In the upper Miocene, however, the genus Procamelus had feet much more camel-like. Procamelus had reached a size somewhat larger than a modern llama, the metapodials were partially fused to form cannon bones, the orbits were completely encircled by bone, the first and second incisors were absent in the adult dentition, and the spacing of the teeth foreshadowed the modern arrangement. Procamelus survived into the Lower Pliocene and displayed the sort of skeletal structure which could become modified equally well into that of a modern camel or a modern llama, although it is very doubtful if a single form can be considered the direct ancestor of both.

The genus Pliauchenia, which represents the Pliocene stage in the grazing line, is represented by a number of large—sometimes very large—llama-like species, not essentially different in structure from Procamelus but with the second lower premolar gone. Before the close of the Pliocene tbe camels had reached India, where species of Camelus are found, and the llamas had reached South America. The precise steps in these two divergent radiations or the exact time when the camels crossed the Behring Straits land bridge into Asia or the ancestral llamas crossed Central America or the Antilles into South America is not known.

Wby one group went north and the other south is an interesting subject for speculation. Perhaps, both spread in both directions together and the one survived in Asia and the other in South America, but no evidence of this has been discovered.

A number of genera of camels are known from the Pleistocene, but several of these by only very incomplete material such as the genus Eschatius and Camelops in North America and Palæolama in South America. Species of Camelus spread westward as far as southeastern Europe (southern Russia and Roumania), and northern Africa (Algeria). Auchenia occurs fossil in the Andean region as well as in Brazil and Argentina. Llama-like forms (Camelops) and what are believed to be true camels (*Camelus americanus*) were still abundant in North America

and the two are found fossil together at Hay Springs, Nebraska, along with the remains of antelopes, horses, and ground sloths.

Why after millions of years of residence the camels should have become extinct in North America during the Pleistocene is one of those problems that remains unsolved, but as both elephant and horse history present the same problem, we look to the future for tbe solution; at the present time, we cannot explain it.

The Horses

Although the evolution of the horse has been described so often that it has become classic, it is so complete and so beautifully convincing that every student should know something about it.

When Macbeth says "Hark! I hear horses," can you imagine substituting the word automobiles for horses? Those who have never heard a group of galloping wild horses or the sound of ridden horses in those backward lands where horseback is the universal mode of travel have missed something for which our modern means of communication are not complete compensation. To understand the outline of horse evolution we have to consider briefly wherein modern horses are adapted.

The principal adaptations are for speed and grazing, the limbs and feet are long and slender, the animal walking on the tip of the third toe. The wrist is what horsemen call the "knee" and the heel of the foot is the "hock." In the front leg the ulna has become greatly reduced and coossified with the enlarged radius which bears the whole weight, and, similarly, in the hind leg the fibula has almost vanished and the tibia or shinbone carries the whole weight. This and the rearrangement of ankle and wrist bones and the formation of keeled instead of smooth joints is an adaptation to prevent the limbs from rotating or becoming dislocated when rapidly moved.

The terminal toe bone (ungual phalanx) is much enlarged and is enclosed in a hoof which is unlike that of any other mammal. The muscles that operate the limbs are largely massed at shoulder and thigh, and slender tendons transmit the force to the distal parts, thus quickening the rate of movement without shortening the stride. Along with these adaptations for speed went a lengthening of the neck, since a grazing animal must easily reach the ground with its mouth unless it develops a proboscis (trunk)

as did the elephants. As in the giraffe, the number of neck vertebræ remains seven, and all are greatly lengthened.

The teeth are very high crowned (hypsodont); they do not close their roots until advanced age and are thus enabled to keep on growing to make up for the wear. The incisors have a deep, enamel-lined pit—the "mark" in their centers, used in approximating the age of a horse by the amount the crowns are worn down. The canines are much reduced and in the females altogether absent. The first premolar has become reduced and of no functional importance and the balance of the premolars

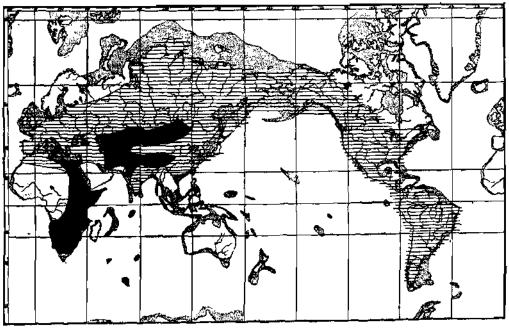

FIG. 156.—Map showing the past and present distribution of the horse family.

have acquired the same size and pattern as the molars. This is complex in its enamel ridges and areas of dentine and cement, so that the surface remains rough with wear and is efficient for grinding the hard food.

This lengthening of the teeth has involved a lengthening of the face and a great deepening of the jaws, with a shifting backward of the eyes beyond the roots of the last upper molars, which is also an advantageous position for a grazing animal. With these evolutionary changes went an increase in size and changed proportions. Increase in size is a great advantage in competition and defense against enemies and, up to a certain point—difficult to estimate in animals—it means increased speed. Sooner or

later, the principle of mechanics that relative strength decreases with size comes into play and this coupled with the increased amount of food necessary to nourish the greater bulk places a natural limit. The Upper Miocene and Pliocene horses were as swift as or swifter than their modern descendants. Certainly, the swiftest living mammals are relatively small, and most of the ungulates have increased in bulk beyond their maximum speed, since speed is but one of the factors making for a successful existence.

The oldest known fossil that can be called a horse belongs to the genus Eohippus (the name means "dawn horse") of the Lower Eocene, of which some 13 different species have been discovered. Eohippus, or the ancestral four-toed horse, can be called a horse only because it is the most primitive type that has as yet been traced in the genealogy of the modern horses. The reader would not recognize it as a horse, and neither did Richard Owen, the great English anatomist, who described its skull from the London clay (Lower Eocene) as Hyracotherium (cony or hyrax-like beast). Structurally, Eohippus can scarcely be distinguished from its contemporaries which represented ancestral tapirs and rhinoceroses. It first appears in the Wasatch formation in numbers, evidently invaded our West from some other region (probably Asia), and nothing is known of its ancestors. The various species ranged in size from that of a cat to a fox terrier.

Not only were these dawn horses tiny but also they had short necks, relatively long bodies with arched backs, the limbs and feet were short, and the hind legs were much longer than the forelegs. The forefeet had four well-developed and functional toes, but the skeleton shows no trace of a thumb, as erroneously supposed by Marsh, and frequently figured as present. The hind feet had three functional toes and vestiges of the first and fifth, so that Eohippus was obviously descended from a five-toed ancestor like some of the Condylarthra. The balance of the limbs was also very primitive. In the front limb the radius and ulna were complete, as were the tibia and fibula in the hind limb. The premolars were simple and the molars had low crowns with six principal cusps arranged in the primitive perissodactyl pattern.

The second stage is Orohippus of the middle (Bridger) Eocene, of which several species are partially known. They were little, if any, larger than Eohippus but the forefeet had the third toe

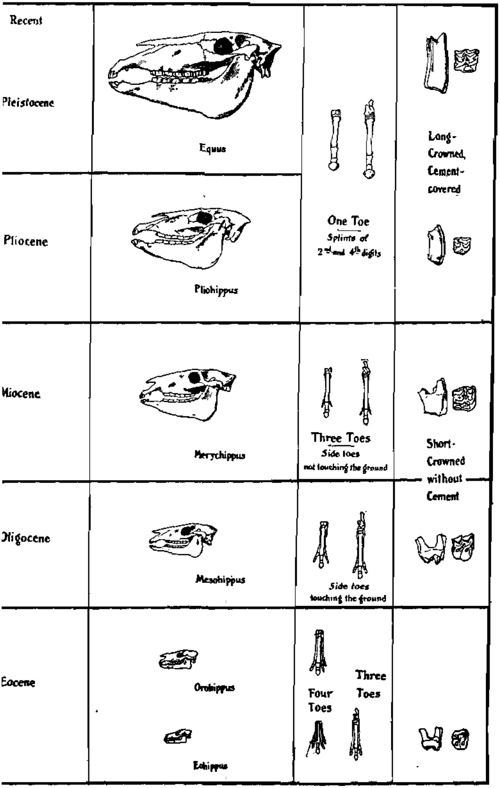

FIG. 157.—Showing stages in the evolution of the skull, feet, and molars in the horse family. (*After Matthew.*)

slightly larger and the vestiges of the first and fifth toes had disappeared from the hind feet. The third and fourth premolar were more advanced and the molar pattern was more pronounced.

The *third stage—Epihippus—is incompletely known. It* occurs in the late Eocene of Utah (Uinta formation). The third toe had increased in size, and the fifth toe of the forefeet was smaller. The last two premolars had become like the molars and the latter had become slightly higher crowned and more sharply crested.

The fourth Stage—Mesohippus—occurs in the lower and middle Oligocene, and the fossil remains of several species are rather common. The size ranged from that of a coyote to a sheep. The cranium was still proportionately large and the face small with shallow jaws. The eyes were not far back and the bony orbits were open behind. The legs were slender; the ulna, although still complete, had become very slender, and the tibia was greatly reduced and partially coalesced with the fibula. All of the feet were three toed with the third or central toe much the largest. The cheek teeth had increased in complexity but were still relatively low crowned and not adapted for hard food.

The next stage—Miohippus—is found in the upper Oligocene and ranges into the lower Miocene. It is much more closely related to Mesohippus than Mesohippus was to Epihippus. It shows little structural change over Mesohippus except that it was a somewhat larger animal and the ankle bones were slightly more efficiently arranged. Although the side toes were now much reduced, they still reached the ground, and some of the descendants of Miohippus, the so-called "forest horses" (Hypohippus and Anchitherium), of both North America and Europe, forsook the plains country for the forests and retained the use of the side toes as aids to support in this soft-ground environment during the Miocene, while the progressive line of Miocene horses had their side toes so reduced that they no longer reached the ground.

The next stage is Parahippus which was abundant during the lower Miocene over a wide range of country. A considerable number of species are known of various sizes, some conservative, and others progressive in either tooth or foot structure. The teeth, in general, became more complicated and higher although still low compared with the Pliocene horses, and the valleys between the crests of the molars began to contain cement.

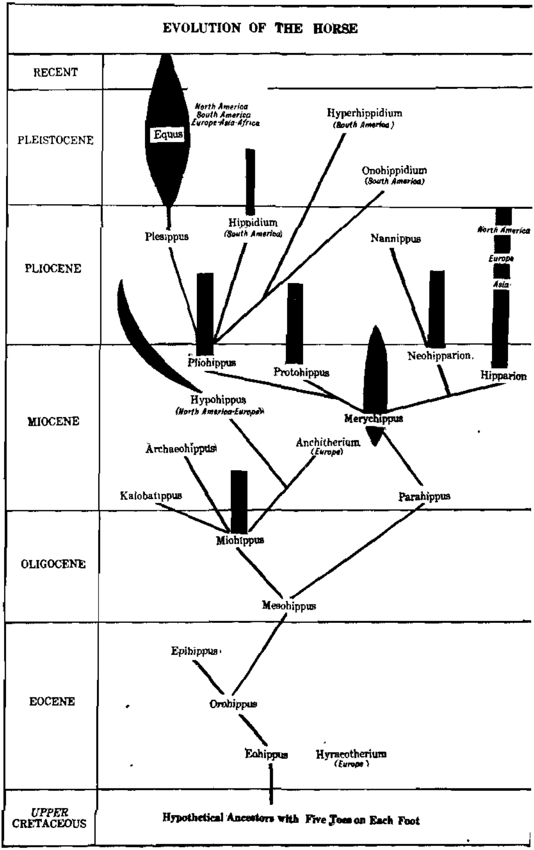

FIG. 158.—The evolution of the horse family (*after Matthew*), entirely North American except where otherwise indicated.

The next stage—Merychippus—appears in the middle Miocene and is closely related to some of the forms of Parahippus. It was very common in the later Miocene and did not become extinct until the early Pliocene. The milk teeth were very similar to those of Parahippus but the permanent teeth, especially in the later species, were progressive and became over twice as high as they were wide and covered with cement.

Among more than a score of known species of Merychippus there is a similar variation in the feet. These were longer than in the preceding stages; the side toes, although still complete, did not reach the ground, and the ulna was ossified to the radius in the adult, though not in the colts.

The next stage—Pliohippus—is a direct descendant of Merychippus. The milk teeth were longer and the adult teeth were also longer and heavily covered with cement, as in modern horses. The head was large and the feet heavier, and the side toes were greatly reduced and may even be absent in some species, so that Pliohippus is frequently spoken of as one toed.

The next stage in the direct line is Plesippus of the Pliocene. It had about the size and proportions of a modern barb but with smaller hoofs and shorter back. The teeth were high and straighter, and prophetic of those of Equus. The feet were very like those of modern horses, with the side toes reduced to splints. The skull had lengthened the face and was also much like modern skulls.

The genus Equus, which includes the modern horses (asses, zebras, etc.), appeared in the record toward the close of the Pliocene and was abundant in the lower Pleistocene of both America and Europe, apparently a direct descendant of Plesippus. It was apparently abundant on all of the continents except Australia and evolved into many species. There were at least a dozen Pleistocene species of Equus in North America ranging in size from *Equus giganteus* of Texas, larger than a modern Percheron stallion, to the tiny Mexican species *Equus montezumæ* and *Equus tau;* some had the proportions of modern asses and some of zebras. Paleontologists are not agreed as to which of these was directly ancestral to the domesticated horse. Only the main stages have been enumerated. Other and collateral lines are shown in the accompanying diagram (Fig. 158). South America has three peculiar genera in the late Pliocene and Pleistocene (Hippidium, Onohippidium, and Hyperhippidium); and

the mainly Pliocene genus Hipparian ranged widely over Europe, Asia, and North America.

It has been seen that North America was the principal theater of evolution of the horse. Why, after millions of years of residence here, it had become extinct before the colonists arrived from Europe no one knows. The various suggestions that have been made are all unsatisfactory, for the few European horses abandoned by Spaniards in the Argentine, southern United States, and Mexico survived and increased to immense herds, thus showing that there was nothing the matter with the environment.

Existing horses comprise a number of species and subspecies as well as many breeds and include the asses and zebras, of which several species are recognized. They are all confined to the Old World and are much alike structurally notwithstanding the very noticeable differences in the appearance of a horse, an ass, and a zebra. Everyone is familiar with these three types so that they need not be described, but they furnish a striking instance of the difficulties of portraying extinct animals in restorations, since the features that make these three types of animals appear so different—length of ears, forelock, mane, character of tail, and color pattern—are all features without clues in the skeleton.

Of the true horses as contrasted with asses and zebras, the only wild species is the Asiatic wild horse—*Equus przewalskii*—a small and not very abundant species of the Gobi region in Asia. The numerous breeds of domesticated horses, ranging in size from Shetland ponies weighing 170 pounds to the larger draft horses weighing 2,400 pounds, are probably all derived by breeding and crossing the descendants of the Neolithic wild horse of Asia with the so-called Arab or Barbary horse of Northern Africa, the wild ancestor of which is unknown but which weathered the Pleistocene glaciations in that favorable region and was, therefore, not affected by the adversities which stunted the Asiatic horse.

All the early horses of history were of this stunted Asiatic type well represented by the present-day Mongolian and Celtic ponies. That was one of the principal reasons why chariots rather than cavalry were largely used in ancient warfare.

The history of the various breeds of domesticated animals is exceedingly interesting but too complicated to be briefly sketched. Students are not agreed as to when horses were first domesticated but this was probably at a very early date in central Asia. Three

different varieties of horses are depicted in the wonderful cave art of western Europe, possibly 25,000 years ago, but it is uncertain whether the Cro-Magnons had tamed them or merely hunted them for food. Evidence of their domestication is found in the later of the lake dwellings in central Europe, and early bronze-age bits have been discovered at a number of localities.

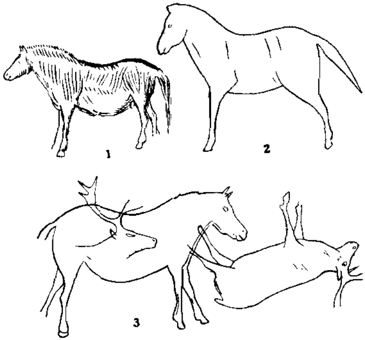

FIG. 159.—Portrayals of horses by artists of the old stone age. 1. Heavy coated horse of the Celtic type. (*After Cartailhac and Breuil.*) 2. Small painted horse. (*After Breuil.*) 3. Incised and painted horse and reindeer. (*After Capitan and Breuil.*)

Some examples of the work of the cave artists are shown in Fig. 159.

PROBOSCIDEA (THE ELEPHANTS)

Although it is as difficult to give a precise scientific definition of the term "elephant" as it is to be sure of the origin of the word itself, which has been attributed to Greek, Hebrew, and Sanskrit roots, almost anyone could unhesitatingly name the outstanding features that characterize the existing animals known as elephants. These would be the hugh body, large head, tusks, and trunk. So thoroughly has this conception become fixed in our language, even though elephants are known to most of us only in captivity and are no longer natives of North America or Europe, that we have an adjective "elephantine" to describe

anything large and heavy, as elephantine proportions or an elephantine tread, elephant apple, elephant fish, elephant beetle, elephant tortoise, etc., and that distressing human disease in which the legs become large and pillar-like is technically known as "elephantiasis."

No animal is more interesting, for the elephant is seemingly so unlike what an animal should be in both appearance and habits that it is a never ending source of wonder and amusement.

Consider, for example, the two most conspicuous things about an elephant—its trunk and its tusks, the latter sometimes weighing over 200 pounds apiece—and imagine all of the adjustments of bone and muscle that makes them usable and useful to their owners and all of the changes that have taken place in them during the past.

If the trunk is considered as an enormously extended nose with one or two finger-like tips at its end, which serves as a flexible elevator to pass food and water to the mouth as well as for seizing and manipulating objects, tossing straw or dirt on the back as protection from the sun's rays, or doing the many things that an elephant does with its trunk, a pretty good idea will be formed of the function of that useful organ.

As a matter of fact, the structure of the elephant as it is formed at the present time could not be improved upon if it had been designed by a most skilful mechanical engineer. The next time that the reader visits any museum where there is a carefully mounted skeleton of an elephant he will find it interesting to verify this statement regarding the elephant body as a machine.

An elephant's legs are like four columns at the four corners of his large body, as tends to be the case in all extraordinarily heavy animals. If the elephant skeleton is compared with the skeleton of a horse, moose, or camel or any other convenient animal in the museum, it will be noticed that the elephant leg bones are not only massive but are also more nearly in a straight vertical line; that is, there is not the angle at the knee and elbow such as is found in most quadrupeds, and the joints or articular surfaces are in a right-angled instead of oblique position. This has obviously been brought about by the animal's increased weight.

Look at the skull, particularly, and notice how it has been shortened from front to back and increased in height, being higher than it is long, which gives it a very "highbrow" appear-

ance. Note, too, what a short neck the elephant has and the long bony processes on the vertebra over the shoulders.

It is easy to see from the skeleton how impossible it would be for an elephant to get his head to the ground and graze or pick up food unless he kneeled or lay down, and if elephants were known only from fossil skeletons, there would be little to serve as a guide in reconstructing the long, mobile trunk on the front of the head, and the conclusion would probably be that elephants had stood around and cropped leaves like the browsing animals with whom we are familiar.

Students of animals use both the term "browsing" and "grazing" in a definite sense for different functions. Grazing is the eating of grass or other herbage from the ground, as do horses, cows, and sheep. Although all grazers are not limited to getting their food in this way but may utilize leaves of bushes or trees, the character of their teeth and lips shows that they are specialized for cropping grass from the ground, and if their ancestral lines are studied, their tooth, jaw, and lip structures will be found to have gradually evolved for this form of food and method of securing it.

Browsing, on the other hand, is the term applied to animals like the rhinoceroses, giraffes, or sloths, that live largely on leaves, which they strip from the branches of trees. They live usually in regions like the forest where everything reaches up and not down for food.

A head like an elephant's, even if it lacked trunk and tusks, could not be carried around on a long neck like that of a horse, and the shortening of the neck shifts the weight backward as near the withers—that is to say, over the front legs—as it is possible to shift it. The shortening of the skull and its great height are the result of the weight of trunk and tusks. Let it be thought of as a simple problem in mechanics: The shortening brings the weight of the lever nearer the fulcrum at the neck and the heightening not only lengthens the power arm of the lever but also furnishes ample surface for attachment of the muscles. If such a skull were sawed through, the bones would be seen as enormously thickened and at the same time lightened by the many cavities that are developed in the bone—as much lightening and inflation as is not conductive to actual weakness, the brain cavity being deeply buried in the back of the skull (that is why it is so extremely difficult to shoot an old elephant in the brain).

The next things to be noted are the teeth in the jaws. Probably, but a single large tooth will be seen on each side in both the lower and the upper jaw, that is, only 4 in all, although there may be traces of others growing in from behind or growing out from in front, for the modern adult elephant has only four active grinding teeth in use at any one time. This is a most curious arrangement, one most perfectly adapted for the lack of space brought about by the shortening of the jaw, and one splendidly calculated to enable the elephants to live to a ripe old age, for no animal in nature can live a day beyond the time its teeth wear out.

Let us write out the tooth formula of our adult modern elephant. *It runs like this:* $i\ \frac{1}{0}$, $c\ \frac{0}{0}$, $p\ \frac{0}{0}$, $m\ \frac{3}{3}$. This somewhat misleading formula requires some explanation, for, as has already been stated, a modern elephant has only 4 teeth at any one time and the formula calls for an incisor on each side of the upper jaw and 12 grinding teeth in all. The two incisors called for are easily explained—they are the tusks, which are, hence, modified teeth. To understand the grinders, a longer explanation is required. Most of the higher animals have two sets of teeth, and all pass through that more or less painful period of losing "milk teeth" as they are called, and cutting the teeth that are to last the rest of a lifetime; the last back molars, that people call the "wisdom" teeth, are often cut so late that their owner has forgotten all about the cutting of his other 28 teeth.

When the baby elephant is about two weeks old he cuts his first real grinding teeth. When these are through the gums, he has the total of 4 already spoken of. These are part of his milk teeth and are used for about 2 years, when they are replaced and shed and their places taken by a second set of 4—the second premolars. These are used until the animal is about six years old when they, now pretty well worn out, are similarly replaced by another set of 4—the third premolars and the last of the milk teeth. The third premolars serve for chewing for about 3 years and are then shed and their place taken by the first of the permanent molars. These last much longer but after 10 to 15 years' use become well worn down, so that when the animal is twenty to twenty-five years old, his second molars replace the first. This set usually serves the elephant until he is about sixty years old and if he has escaped disease and accidental death he gets his last set of 4 grinders, which last for from 40

to 60 years, and when they are worn out he will die of starvation at a ripe old age of somewhere between one hundred and one hundred twenty years.

The little diagram (Fig. 160) shows the arrangement of the molars in one half of the upper jaw of an Indian elephant about twenty-five years old. The root of molar 1 is still to be seen behind the tusk and in front of molar 2 which is now doing the work of chewing. Molar 3 is gradually developing beneath the gum and behind molar 2. This will grow slowly and in about 35 years will take the place of molar 2.

FIG. 160.—Section through the middle of the skull of an Indian elephant about twenty-five years old, showing base of tusk, remnant of worn-out molar in front, chewing grinder, and an uncut molar behind.

A single grinder has a peculiar structure, especially fitted to give such long service in grinding coarse, wearing food, not exactly like the teeth of any other animal. In the first place, the elephant's grinders are much larger than those of any other animals. They are made up, as can best be seen by cutting a tooth in half, of 10 to 27 vertical plates or folds of ivory (dentine) surrounded by a layer of enamel and set into a solid mass of softer cement. This alternation of hard ridges and softer valleys keeps them from becoming smooth and inefficient when they wear down.

Figure 161[2] shows a grinder of an African elephant one-fourth natural size, the black loops on the grinding surface being the enamel. Notice the great height of the whole tooth, the width of the enamel loops, and how the front part, which came into use before the hinder part and has had much longer wear, is ground down almost to the roots. When the hinder part is similarly worn down, the front part will be gone entirely, the tooth will have moved forward in the jaw, and the time will have come for another tooth to replace it.

Figure 161[1] shows the appearance of a grinder of an Indian elephant, which has been sawed through the middle. This is in

about the same stage of wear as that of the African elephant shown in Fig. 161.[2] The solid black part is enamel, the white is dentine, and the cross-lined part is the cement. It will be noticed that there are more enamel folds than in the teeth of the African elephant. Those at the front end are worn down about as far as in Fig. 161,[2] but at the hinder end will be seen three of these folds that will not come into action until the grinding surface is worn down an inch or two more.

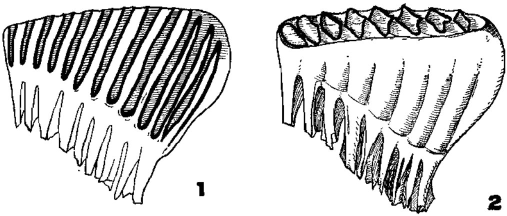

FIG. 161.—Sections of molar teeth of African and Indian elephants, one-fourth life size. 1. Indian elephant. 2. African elephant.

Of course, it is not easy to recognize the more ancient ancestors of the elephants, since millions of years ago the ancestral horses, rhinoceroses, elephants, or tapirs—the thick-skinned, herbivorous animals that naturalists call Ungulates—were scarcely distinguishable from one another in either structure or habits, and it is sometimes difficult to tell whether a given specimen should be called a rhinoceros or a tapir. It is only by tracing the successive modifications backward step by step from existing forms that it is possible to arrive at a solution of the problem.

Fossil skeletons or parts of skeletons, especially teeth like those of modern elephants, were among the earliest discovered in both America and Europe. Hippocrates, sometimes called the "father of medicine," had one, and this is easily understood, as will be seen later, when it is realized how abundant elephants were all over the northern hemisphere in the closing days of geological time. Gradually, men learned of many kinds of fossil elephant-like animals in the more distant past in North America, Europe, and Asia, but students were long puzzled to know on what continent they originated or what their earlier

ancestors were like, for they seem to have appeared rather suddenly in Europe at a certain time, and there was no means of knowing whether they had immigrated into Europe from Asia or Africa or even that their earlier ancestors might not have remained undiscovered and hidden in the rocks of the Americas.

In 1898, the Geological Survey of Egypt commenced to survey the Libyan Desert in northern Egypt and in the region known as the *oasis of the Fayûm*—from an ancient Egyptian root word meaning "lake," about 50 miles southwest of Cairo—the beginning of the solution of the problem of the birthplace and nursery of the elephant appears to have been solved.

This oasis bristles with human as well as geological history. It is a natural basin lying west of the Nile. Its human history begins before the dawn of Egyptian civilization when the men of the old stone age frequented it and left their flint implements over its surface. Coming down to later times it is found that Amenemhat I built irrigation works here some 2,200 years before Christ. Later on, there were Greek and Roman cities in the oasis, as attested by their ruins which are still standing. The Ptolemies built storage reservoirs here, at a time when the lake was known as Lake Mœris. This lake is now shrunken and salty and is known as Birket-el Qurûn.

The scientific name of the earliest known ancestral elephant—Mœritherium—is compounded from Lake Mœris and the Greek word *therium* meaning "animal," thus: "Mœris beast" in English. At the time that this dawn elephant flourished in northern Africa the country was very different from the Egypt of history, and a greater river than Mother Nile, which seems so ancient, emptied into the Mediterranean sea at this point, or about 150 miles south of the present delta of the Nile, for at that time the Mediterranean Sea was much larger than it is at present and flooded all of the country which we know as northern Africa.

This was millions of years ago, long before there were any human beings on the earth, a period which geologists have named the Eocene. The geological times that we pass through in considering the history of the elephants, that is, our geological time clock or time table, comprise, from oldest to youngest, what geologists call Eocene, Oligocene, Miocene, Pliocene, and Pleistocene, the last being the ice age or glacial period which immediately preceded our own period—the Recent, or the age of man.

At the remote time when Mœritherium lived, northern Africa was a Garden of Eden compared to its present-day aridity. The land was forested with tropical trees some of which, in a petrified condition—that is, changed to stone—and of large size, are still to be seen. A variety of animal bones have been found, none of which is more instructive than those of Mœritherium, our ancestral elephant (Fig. 162).

This was a small, swamp-dwelling animal about the size of a tapir or pig; the neck was long enough to enable the head to reach the ground. The very obvious marks left on the skull by the trunk in the later elephants are wanting, showing that it had no trunk. The skull is long and narrow; the body is

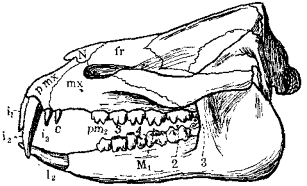

FIG. 162.—Side view of the skull of Mœritherium lyonsi, one-fifth life size. (*After Andrews.*)

long, with 20 pairs of ribs; and the leg bones are slender. The most fascinating features are the teeth, which stamp this small and ancient animal as a potential elephant.

First of all they are 36 in number, with this formula $i\ \frac{3}{2}$, $c\ \frac{1}{0}$, $p\ \frac{3}{3}$, $m\ \frac{3}{3}$. The grinders are of the ordinary mammalian type, small, with 4 cusps or bumps on the grinding surface, and lacking the height and folds that characterize elephant teeth. The most remarkable feature is that 2 of the upper and 2 of the lower incisors or cutting teeth (the second) are enlarged to form incipient tusks, the first and third incisors and the canines being reduced and simplified and scarcely, if at all, functional.

The small upper tusks are directed downward and the lower tusks forward, as shown in the picture. Here we have nothing of the elephant except the makings as it were in the prophecy of tusks shown by the enlargement of the 4 tusklike incisors and the reduction of the rest of the teeth in the front of the mouth. This beast lived in Upper Eocene and Lower Oligocene time.

This question of the elephant's ancestral home seeming to be definitely settled, there was subsequently found what appears to be another Mœritherium in rocks of about the same age or slightly younger in India, so there is still some uncertainty as to whether northern Africa or southern Asia was the starting point, but these two regions were evidently in communication at that early time, before the Arabian Desert had come into existence, and it is surely interesting to find the earliest elephants in the two regions where modern elephants are still found, after their aneestors had spread very nearly over the whole world.

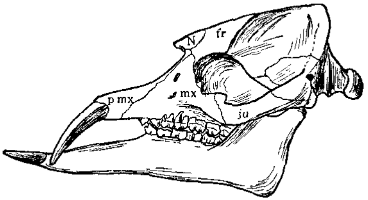

FIG. 163.—Side view of the skull of Palæomastodon, one-eighth life size. (*After Andrews.*)

The second stage of elephant evolution, still more prophetic of what the future was to bring forth, is found at higber levels in this same Fayûm region, associated with the skeletons of the later Mœritheriums. This second stage of development, represented by a variety of different-sized forms, is called the Palæomastodon, from two Greek words meaning "ancient mastodon." Palæomastodon (Fig. 163) was considerably larger than his ancestors and ranged in size from that of a tapir to that of a modern half-grown Indian elephant. The neck was still relatively long, though the hinder neck vertebra had commenced to shorten; and although the leg bones were more massive, they were still light for an elephant. From the position of the eyes and of the nasal openings it may be inferred that the animal had a short trunk or mobile snout.

The tooth formula is $i\,\frac{1}{1}\;c\,\frac{0}{0}\;p\,\frac{3}{2}\;m\,\frac{3}{3}$, from which we see that Palæomastodon had four tusks, now of considerable size, as can be seen in the picture; that the rest of the teeth in the front of the mouth had disappeared as well as one lower pair of premolars;

but that the jaws were still long enough to permit the milk grinders to be replaced by the permanent set of grinders of which all 22 were retained thoughout life and were used in the usual way that animals chew. The grinders had increased somewhat in size and added 2 cusps to their grinding surface, making 6 cusps in all.

At this point there is a break in our history due to the fact that no other Oligocene elephants have been discovered except an Indian form very like Palæomastodon and known as Hemimastodon, so that the record of some thousands of years or more is missing, during which time the developing elephant line probably did not spread beyond Africa and southern Asia, for the exodus from Africa into Europe appears to have been at the beginning of Miocene time. During this time is introduced a great variety of elephants, and before its close they are found in Europe, Asia, and North America, for once they started they were not surpassed as travelers by any other animals except the horses.

There is some difficulty in presenting this later elephant history in a simple way because naturalists have differed in the skeletal characters that they have emphasized in classifying and naming them—some relying on the structure of the grinding teeth and others on the number and character of the tusks. First are found much larger four-tusked forms in Tunis and then in Italy; by way of Asia and across Behring Sea, which was then dry land, they reached North America. In some, the upper jaw was shortened, in others, the lower jaw; and, eventually, there emerged two quite different forms, one with the long trunk and long upper tusks like a modern elephant, and the other in which the lower tusks became recurved and the upper tusks disappeared. This last, known first in India, then in Africa, and, finally, in Europe, is called a Dinotherium and became extinct before the close of the Pliocene.

The Miocene elephants were what might be called "mastodons" instead of true elephants, the distinction between the two being largely a matter of the structure of the teeth. At this time, they had reached about the size of a modern Indian elephant, but still retained the four tusks, although the lower ones were much reduced in size. The neck had become much shortened and the teeth had so increased in size that but two grinders at a time were present in each half of each jaw, that is, eight in all.

Elephants were now widespread and diversified. In Eurasia there arose modified forms which lost their lower tusks and in which the upper tusks lost the enamel bands on them that proclaimed that they were modified teeth. These were the ancestors of the American mastodon. In North America they gave rise to a two-tusked form which retained the enamel bands on the tusks and were the first of the stock to cross southward into South America, where they spread to the southern end of that continent. In southern Asia modified forms during the late Miocene are thought to have been the starting point of the true elephants with the peculiar tooth features or the modern elephant.

These spread westward into Europe and eastward into North America at the same time that the mastodon was spreading from Europe into North America. This happened during what geologists call the Pliocene, which brings us to the latest geological age following the Pliocene and immediately preceding the present, which geologists call the Pleistocene. This was the time of snow and ice in northern Europe and North America—the time when early man first appeared on the scene—hence, it is sometimes called the "glacial period" or "ice age" or the "age of man."

In North America were four elephants—the very abundant mastodon and three different true elephants, or "mammoths," as they are called. The latter were the largest elephants that had ever existed before or since—the imperial mammoth being 13½ feet tall at the shoulder and having tusks 13 feet or more in length. One of their huge fossil teeth is about all you would care to carry any distance and was considerably larger than the teeth shown in Fig. 161.

The American mastodons were not so tall but were extremely bulky, and their hairy covering made them seem still more so. Their skulls sometimes show traces or small vestiges of the lower tusks, especially in the males. They outlived their Old World ancestor and their bones and teeth have been found from Alaska to Florida and Central America. They are believed to have been still living in North America when the first men arrived from Asia.

The Old World mammoths are more interesting than those of the New World for two reasons. First, because, although not quite so large, they lived on in Europe to a time not more than 15,000 to 20,000 years ago, when they were drawn and painted

by the cave-dwelling artists of that time; and, second, because several specimens have been found frozen in the frozen soil of northern Siberia, where the cold has preserved them in a natural icebox for thousands of years.

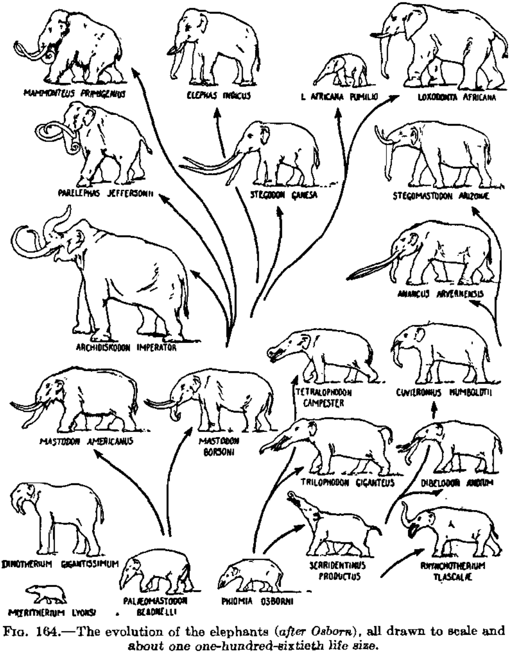

FIG. 164.—The evolution of the elephants (*after Osborn*), all drawn to scale and about one one-hundred-sixtieth life size.

As long ago as 1696, a Russian described some of their bones, which are exceedingly abundant in Siberia and which the Tartar peasants believed to be the bones of a gigantic mole, called "mamantu" or "ground dweller," which always died when it

unwittingly came to the surface of the ground, where the light was fatal. This rude slavic word was the origin of our name "mammoth" for these animals, latinized as *mammut* and frenchified as *mammouth*.

These elephants must have been exceedingly common throughout the Northern Hemisphere, for their bones are so common in Siberia that there is considerable commerce in their tusks. Before the World War, about 1,600 tusks, with an average weight of 150 pounds, were exported from Siberia in a single year, making an annual export of over 100 tons of ivory.

Similar bones and fossil ivory are not uncommon in Alaska, and the fossil teeth are so abundant in northern Europe that the English fishermen on the North Sea bring up hundreds of teeth in their trawls from the Dogger banks of which so much was heard during the World War, for the Dogger banks are a favorite fishing ground and were not beneath the sea during the Pleistocene but were part of the land over which the elephants and other land animals, including man, roamed at will.

Several of these frozen elephant carcasses have been found in northern Siberia by ivory hunters who have chopped off the tusks and partly dug them out to rot or become the prey of wolves. One of these finds was brought to St. Petersburg (now Leningrad) in 1806 where it is now mounted in the Zoological Museum with scraps of the hide sticking to the bones. It seems to have been complete when first discovered in 1799, and the ivory merchant at Yakutsk who saw it said that the body was then fairly complete, with the trunk and ears, and long coarse hair.

A second frozen elephant was found about 800 miles west of Behring Straits in 1901, and this was not allowed to be destroyed, but the skin is mounted in the Leningrad Museum in the attitude in which it was found. It seems that the huge beast had fallen through a crevasse in the ice, possibly masked by an overgrowth of vegetation, just as today one can see vegetation covering the lower part of the Malaspina Glacier in Alaska. The fall broke the poor brute's hip and one of its forelegs and in its violent struggles to escape it burst a blood vessel, as was shown by finding a mass of clotted blood in the chest. This beast received a very thorough study even to determining the names of some of the grasses and other plants found in its stomach and in the unchewed mass that it had been eating at the time of the accident.

These hairy mammoths of cold countries are probably better known than any other fossil animals, and even if their frozen remains had not been discovered, contemporary evidence would not be lacking of their general appearance and hairy condition, because they were a favorite subject for the remarkable artists of the old stone age, who drew them in most lifelike postures on the walls of their caves or engraved them on deer antlers or fragments of tusk ivory. The accompanying illustration (Fig. 165) shows copies of three of these ancient works of art. The standing mammoths are from two caves in western France and

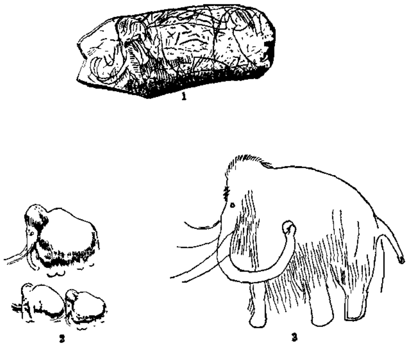

FIG. 165.—Drawings of the hairy mammoth by artists of the old stone age.

the charging mammoth is engraved on a fragment of a tusk from the same region.

The existing elephants are found in Africa and southeastern Asia. Those of Africa are of several kinds and are descended from European Pleistocene ancestors. Those of Asia are descended from Indian Pleistocene ancestors and the female is usually without tusks. The African elephants are larger than the Indian and will sometimes weigh over 7 tons. They have much larger ears, bigger tusks, and two instead of one finger-like process at the end of the trunk.

All modern elephants live in the jungle and are, hence, hairless. Like all forest animals, their sight is poor, but their senses of

smell and hearing are very acute. They have many interesting habits; the Asiatic ones are especially docile and obedient in captivity and have been used since early historic times as beasts of burden.

They are rather timid generally, but when brought to bay, rage may give them courage and make them formidable and dangerous foes. Old males, also, get surly and dangerous. In this state, they are expelled from the herd and lead a solitary and murderous existence, being known as "rogues" and avoided,

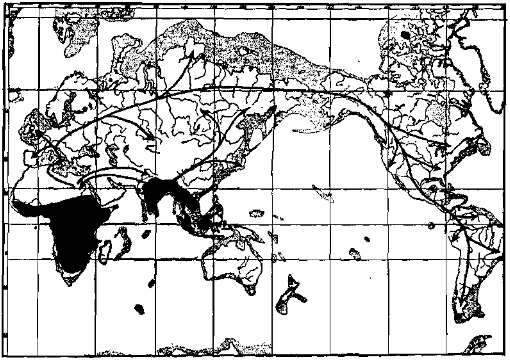

Fig. 166.—Map showing the distribution of the elephants at the present time (solid black), their distribution in the past, and the probable directions of their dispersal.

if possible, by hunters. In captivity, similar old males get more and more intractable until some fine day they will attempt to kill or succeed in killing their keeper, when they have to be destroyed.

Elephants do not seem to mind the cold particularly, nor are mountains a barrier to their spread, unless these are exceptionally high and difficult. They crossed the Alps with Hannibal's army during the Punic wars but apparently could not cross the Pyrenees between France and Spain during the Pleistocene.

The tusks started as digging organs, and although their large size in the later forms might suggest that their sole use was for

fighting, the way the tips are worn shows that they were much used in the primitive way. Fossil tusks are also much worn at the points, one usually more than the other, and this wear is especially marked in the tusks of the northern mammoth which had to dig to find its food through the snow and ice that covered so much of the ground.

A small map of the world (Fig. 166) has been printed as an aid in seeing how small an area is occupied by the existing elephants as compared with the extent of country that they ranged over during their past history. The arrows indicate in a simplified way the routes by which they originally spread from continent to continent.

The Rhinoceroses

The rhinoceros-like animals comprise a large and complicated group of odd-toed animals which show a great variety of progressive adaptations in several directions, so that authorities differ considerably in interpretations of their mutual relations.

They are another one of those groups that are utterly foreign to North America in the existing fauna but which were a prominent element of the North American fauna from the Eocene until the Lower Pliocene—an inconceivably long time—and which several eminent students of the group believe to have originated in North America, although others favor southwestern Asia as the site of their original home.

During the Middle Ages, the only known living rhinoceros was the single-horned Asiatic one and this received its name from the Greek *rhino*, "nose," and *keras*, "horn," appropriate enough for the living rhinoceroses but not quite so fitting for the great variety of Tertiary hornless forms. The specific name of the Asiatic form was the Latin *unicornis*, or "single horned," and this same beast was undoubtedly the basis of the legendary unicorn of the ancients. When central Africa began to be known, two-horned rhinoceroses were discovered, and the first of these was christened *bicornis* or "double horned."

The modern rhinoceroses are found in Africa, southern Asia, and the larger islands of Malaya (Sumatra, Java, and Borneo) (see Fig. 167) and they are now separated into four genera—Diceros and Ceratotherium in Africa, Rhinoceros and Ceratorhinus in Malaysia. These represent the end products of several

independent lines of descent. Before discussing the fossil forms, a consideration of a few of the adaptations of these existing Old World genera is desirable.

All of the existing rhinoceroses are large and massive, long-bodied animals, and all have solid dermal horns except the females of *Rhinoceros sondaicus*. The Indian and Javan species have a single nasal horn; the African and Sumatran species have an additional horn on the forehead. These horns are solid

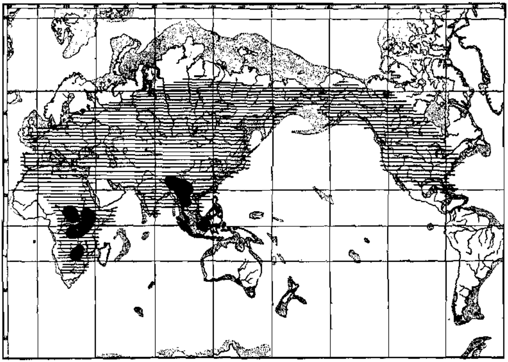

FIG. 167.—Map showing the present (black) and past (lined) distribution of the Rhinoceros family.

masses of hairlike fibers; they are true dermal structures and do not have cores of bone as do the horns of most ruminants (cattle, antelopes, etc.). The skulls, however, give evidence of the presence of horns, not only by the shape and thickening of certain bones but also by forming roughened areas on the bones over which the horns are located.

Rhinoceros skins are exceedingly thick—a protective adaptation—and are usually hairless. The Indian rhinoceros has the skin unusually thick and with regular folds in it, giving the animal a very peculiar appearance. All of the existing rhinoceroses, except the so-called "white" rhinoceros of Africa, are browsers and frequent forests and marshes. The "white" rhinoceros is a

grazer and, hence, frequents more open country than its fellow countryman, the black rhinoceros (*Diceros bicornis*).

Although the existing rhinoceroses differ in size, proportions, and details of appearance, all have short necks, long bodies, and

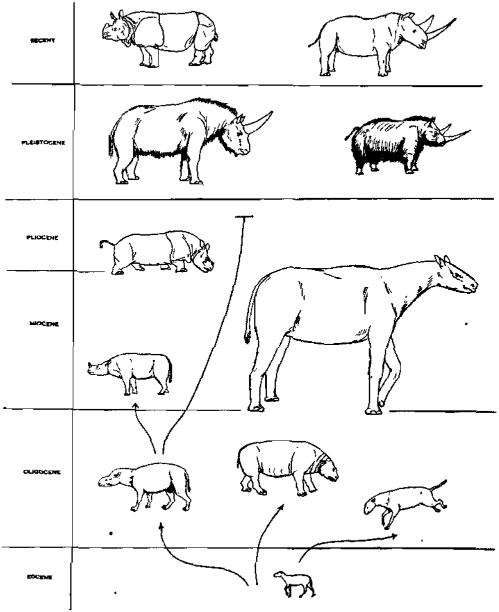

Fig. 168.—Some stages in Rhinoceros evolution. (*After Osborn.*)

short, stout limbs and feet, as, indeed, do all very heavy animals. All of the feet are three toed. All except the African grazing species have pointed muzzles and a prehensile upper lip (inflexible in the Sumatran species), which is a browsing adaptation. The teeth of all are similar and highly characteristic. In the African

Ceratotherium the incisors and canines have been lost. All of the others have a pair of chisel-like upper incisors and a pair of long, forward-directed, tusklike lower incisors. All of the premolars except the first are essentially molariform, and the molars are not high crowned except in the African grazing species. The dental formula for all except Ceratotherium is $i\,\frac{1}{2}$, $c\,\frac{0}{0}$, $pm\,\frac{4}{4}$, $m\,\frac{3}{3}$. The molars have two oblique transverse crests and branches projecting inward from the outer borders of these crests.

The skulls show characteristic adaptations for carrying and manipulating the horns, such as the enormously thickened and elevated nasal bones. The cranium is widened and thickened with air chambers for lightness. The lower leg bones (radius and ulna in the forelimbs, tibia and fibula in the hind limbs) are separate and well developed, as in all massive straight-limbed ungulates; and the foot bones are extremely short and massive.

Turning now to the fossil forms, it is found that there were a great many species; well-preserved fossil skeletons are not uncommon and, for some species, may fairly be said to be abundant. There have been discovered 4 Eocene, 11 Oligocene, 8 Miocene, 6 Pliocene, and 5 Pleistocene genera. As there are 4 living genera, the progressive reduction of kinds with the passage of time after they had attained their first diversification in the Oligocene is impressive.

As has already been stated, rhinoceros history comprises several independent lines of adaptation, so that it will be clearer to sketch each one separately. The three main lines of evolution are (1) the heavy, slow, browsers, chiefly of forest glades and marshlands, what might be called the "true rhinoceroses;" (2) those which remained light and slender and became adapted for cursorial life, running away from their enemies; and (3) a series of Eocene and Oligocene forms which became adapted for an aquatic or semiaquatic existence, perhaps comparable with the mode of life of a modern hippopotamus.

In all of these lines the history is not that of one progressive series, but a variety of progressive and conservative strains exist contemporaneously. Thus, the rhinoceroses are an especially good example of what naturalists call a "polyphyletic group."

Hyracodonts or Cursorial Rhinoceroses.—The oldest fossils which can be referred to rhinoceros ancestry with any certainty comprise a group of small, cursorial forms constituting the sub-

family Hyracodontinæ,[1] and these are unknown outside North America, where they range from the middle Eocene (Bridger formation) through the Oligocene (White River formation).

The oldest known genus is Hyrachyus which appears at the base of the middle Eocene (Lower Bridger formation). A great many species have been described ranging in size from that of a fox to that of a modern tapir. Possibly, among these as they become better known may be found the ancestors of the other two main lines of rhinoceros descent, although this has not yet been demonstrated.

Like all ancestors, Hyrachyus was what might be called a "generalized perissodactyl;" that is, its specialization was a matter of the future. It is this generalized character of all of the early Tertiary mammals that makes it so exceedingly difficult to distinguish among the different lines—horse, tapir, rhinoceros, lophiodont, etc.—thousands of years of adaptive divergence had to take place before their differences became marked.

Hyrachyus had a relatively long body, short neck, and moderate limbs; the feet were not especially long and were four toed in the front pair and three toed in the hind pair. The skull was long, narrow, low, and hornless, the nasal bones being thin and straight. No incisors had either been modified or lost; the canines were of moderate size; the premolars were smaller and simpler than the molars; and the latter were rhinoceros-like in the upper jaw and rather tapir-like in the lower jaw.

[1] The beginner is often confused by the variations in the classifications of different specialists in all groups of organisms. Thus, Osborn arranges the rhinoceroses in two families and eight subfamilies as follows:

Superfamily Rhinocerotoidea:
- Family Hyracodontidæ—the hyracodonts:
  - Subfamily Hyrachyinæ—cursorial rhinoceroses.
  - Amynodontinæ—aquatic rhinoceroses.
  - Hyracodontinæ—true hyracodonts.
- Family Rhinocerotidæ—true rhinoceroses:
  - Subfamily Aceratheriinæ—aceratheres and diceratheres.
  - Teleoceratinæ—teleoceratines.
  - Rhinocerotinæ—rhinoceratines.
  - Elasmotheriinæ—elasmotheres.
  - Baluchitherinæ—baluchitheres.

The more conservative classification adopted for this book is as follows:

- Family Rhinocerotidæ:
  - Subfamily Hyracodontinæ.
  - Amynodontinæ.
  - Rhinocerotinæ.

Hyrachyus gave rise to a contemporary form known as Colonoceras, which developed a small pair of horns on its nasals, but it did not survive the middle Eocene, whereas a second derivative of Hyrachyus, namely, Triplopus, ranges from the middle to the upper Eocene. Triplopus was a slightly larger animal with lighter limbs and had but three front toes, one having disappeared. The whole skeleton of Triplopus is not known, but it is believed to constitute a link between Hyrachyus and the common Oligocene Hyracodon.

Hyracodon was somewhat taller and more stocky than a modern sheep. The hyracodonts had long necks carrying relatively large heads. The body was long but not heavy, and the limbs were relatively longer and more slender than in the later rhinoceroses and not unlike those of the Oligocene horses (Mesohippus). Each foot had three toes of which the central one (the third) was much enlarged and the second and fourth were much reduced, so that if the hyracodonts had not, for some unknown reason, become extinct in the Oligocene but had continued down to the present along the same evolutionary lines, they would undoubtedly have developed into single-toed animals.

Despite their superficial resemblance to the Oligocene horses, their structure stamps them as rhinoceroses. This is shown by the limb bones, the elongation being in the forearm and thigh; by the short, high, and thick skull; and, especially, by the teeth. The low molars are of the rhinoceros pattern; all except the first premolar had become like the molars; the incisors and canines were small and simple. Why the defenceless hyracodonts became extinct in the Oligocene while the equally defenceless and hardly fleeter-footed horses lived on is another one of those paleontological riddles.

Amynodonts or Aquatic Rhinoceroses.—The amynodonts (subfamily Amynodontinæ) comprise a series of forms which by a succession of adaptations from some small, Hyrachyus-like animal had developed larger, stouter bodies and larger canines before the close of the middle Eocene. They illustrate a principle in toe reduction which explains a condition that holds for all perissodactyls—namely, that small, active forms tend to have the toes reduced in number but that with increase in size, a point is reached where continued reduction would be disastrous, and, therefore, no further reduction takes place. Thus, when the primitive amynodonts waxed heavy, they continued to the end

of their history with the same number of toes that they had at that time, that is, four on the front feet and three on the hind feet.

In the upper Eocene the genus Amynodon shows larger and heavier species than in the middle Eocene, animals in which the canines were further increased in size. The premolars were still all present, although considerably smaller than the molars, and only the last two had the molar crown pattern. The genus Amynodon was succeeded in the lower and middle Oligocene by the genus Metamyodon.

The bones of Metamyodon occur almost exclusively in the consolidated sands of Oligocene river channels known as "channel sandstones," and this fact, coupled with the position of the eyes and nostrils and certain other structural features, indicates that in life they were semiaquatic and had habits much like those of the present-day hippopotamus. Metamyodon was the largest rhinoceros of its time, relatively long bodied and thickset, with short, thick neck and short limbs, four toes in front and three toes behind. The incisors were all present but neither enlarged nor reduced. The canines had developed into tusks, the upper short and heavy, the lower very large. The premolars were small and one upper and two lower pairs had disappeared. The molars had the rhinoceros crown pattern but were narrow. The tooth formula was $i\ \frac{3}{3}$, $c\ \frac{1}{1}$ $pm\ \frac{3}{2}$, $m\ \frac{3}{3}$. The skull was considerably modified, being depressed with a shortened face, heavy arches, and a high sagittal crest. No horn was developed.

Metamyodon was the last American member of its race and apparently became extinct, perhaps because of a change in climate. Meanwhile, some of the amynodont race had reached the Old World, for there are two Oligocene genera (Ronzotherium and Cadurcotherium) found fossil in Europe and Asia, whose relationship to the American forms is obscure. Why the clumsy amynodonts should have gotten so far from home and the less specialized and fleet hyracodonts did not, is another problem whose answer we do not know. Perhaps the latter did and specimens will eventually be discovered in Asia and Europe, just as Titanotheres—long thought to be exclusively American—have been discovered in Mongolia in recent years.

Rhinocerotinae or True Rhinoceroses.—The subfamily Rhinocerotinæ embrace what are often called the "true rhinoceroses" to distinguish them from the hyracodonts and amynodonts. They begin their history in the North American Oligocene and

they are represented here through the Miocene and as late as the lower Pliocene. Some early members of the race wandered to Asia and Europe, and it was the descendants of these emigrants which were the ancestors of the existing rhinoceroses.

The oldest known representative of this line is the genus Trigonias of the Lower Oligocene. Trigonias, as was true, also, of most early rhinoceroses in both America and Europe, was without horns. The skull was, consequently, flat and its bones relatively thin. Although of a heavier build than the hyracodonts, the body and limbs were not massive. A primitive character was the presence of four toes on the front feet, for although the first toe had completely disappeared and the third toe was much the largest, the fifth was still present and functional but much reduced in size and on its way to elimination through disuse. The teeth were quite rhinoceros-like: thus, the first upper incisors had the chisel shape so characteristic of later forms, but the other upper incisors were also present, as well as a small canine. In the lower jaw, also, all the incisors were present and the second pair was enlarged and somewhat tusklike, but the lower canines had disappeared. Hence, the tooth formula was $i\,\frac{3}{3}$, $c\,\frac{1}{0}$, $pm\,\frac{4}{4}$, $m\,\frac{3}{3}$.

The next stage is illustrated by the genus Cænopus of the Middle Oligocene. Cænopus was hornless and much resembled a modern tapir in size and proportions, that is, it was much less massive than a modern rhinoceros. Conclusions of this sort are deduced from the general proportions of the skeleton and its parts, such as the length and curvature of the ribs, width of the thighs, and the diameter of the limb and foot bones. All four feet in Cænopus were three toed as are the feet in all later American forms and all living rhinoceroses.

Trigonias and Cænopus are representatives of a line of rhinoceroses which were entirely hornless or which developed only rudimentary frontal horns, a line which extended its range from the western United States to Asia and Europe and which continued to exist without any very essential changes except a gradual increase in size through the Miocene and Pliocene, surviving in North America as late as the Middle Pliocene (genus Aphelops) of the Western states and Florida.

This essentially hornless line is known as the Aceratherium line, and its later members are almost as large as the existing Indian rhinoceros. Along with the Oligocene acerathere we

find the remains of a second and remarkably short-lived line of evolution, which apparently had its origin in a common ancestry. This line is that of the "diceratheres," so named because they developed a pair of small horns on the nasals. The diceratheres are present in the Middle Oligocene and become well characterized in the Upper Oligocene, and they have been found fossil in western North America and western Europe.

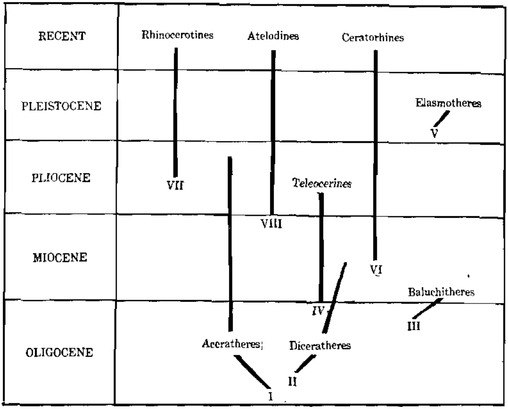

FIG. 169.—The eight lines of true Rhinoceroses of the Tertiary and Recent.

The diceratheres (genus Diceratherium) greatly resembled the contemporary aceratheres in size and proportions, with relatively slender bodies, fairly long limbs, and well-developed incisor tusks. All of the known forms are three toed and could evidently get over the ground with considerable speed. They differed from all other known rhinoceroses in the pair of small nasal horns. These were sometimes quite rudimentary and were apparently developed rather late in life and then only in the males in the Middle Oligocene forms but were better developed and apparently in both sexes in the Upper Oligocene forms. They are frequently spoken of as the "pair-horned" rhinoceroses, for in all other known rhinoceroses which had two horns, one is

behind the other, tandem, and not side by side. The diceratheres for some unknown reason, did not survive in the struggle for existence, and they disappear from the geological record in the Lower Miocene.

Thus, there were two well-defined lines of true rhinoceroses as early as the Middle Oligocene; and there must have been more than two, for the queerest of all rhinoceroses that has yet been dug out of the rocks is found in the late Oligocene or early Miocene of Asia and represents a third diverging line, that of the baluchitheres. Fragmentary parts of this remarkable beast were discovered in Baluchistan in 1911—hence, the name Baluchitherium or "Baluchistan beast." Later they were found in Turkestan, and, more recently, in Mongolia. Much of the skeleton remains unknown so that there is considerable conjecture about the accompanying restoration, but we know the teeth, neck vertebræ, part of the limbs and feet, and most of the skull.

This giant rhinoceros makes the largest living rhinoceros—the "white" rhinoceros of Africa—look like a pygmy, and it is more than twice the size of the Pleistocene Elasmotherium which was a third larger than the white rhinoceros. Baluchitherium is estimated to have been 13 feet high at the shoulders, with a massive, elongated neck and a long, narrow head, and capable of browsing on twigs 16 feet above the ground. The legs and feet were elongated and the feet had three toes. The skull was well over 5 feet long, convex and narrow, and without indications of horns. The second incisors were formidable tusks and the molars were low crowned. On the whole, the skeleton shows sufficient ancient features to lead to the conclusion that Baluchitherium was probably derived from some early member of the acerathere line. Despite its size, it is thought to have been a somewhat speedier animal than a modern elephant.

A fourth line of rhinoceros descent, known as the Teleocerine (end horned) or brachypodine (short footed), makes its appearance in the Lower Miocene of western Europe and is, therefore, supposed to be of Old World origin. By Pliocene time it had spread as far as western North America, where it roamed in large herds until the beginning of the Pleistocene or, perhaps, slightly later. The teleocerines had massive bodies, sharp tusks, extremely short legs, and a low, sharp horn on the end of the nose. Thus *Teleoceras fossiger*, found in Kansas, although it was 10 feet long and had a girth of over 9 feet, was only a trifle

over 4 feet tall at the shoulders. These proportions suggest that the teleocerines haunted river banks and swamps and had habits comparable to those of a hippopotamus.

A fifth line, of which we know only its end member—the giant elasmothere of the Pleistocene—has been found in Europe and Siberia and was a dweller in the cold climate of the ice age. It was the largest known rhinoceros until Baluchitherium was discovered. Elasmotherium (the name is in allusion to the thin, frilled cusps of the high-crowned molars) was a fairly long-legged massive beast with a skull a yard long. It had no nasal horn but did have a huge horn in the middle of the forehead, which suggests that some day its ancestors will be discovered among the Miocene aceratheres. Elasmotherium was a contemporary of the hairy mammoth and, like the latter, was probably provided with a thick protective covering of hair and wool. It was evidently a grazer—in fact, trees were scarce at that time in the region where it dwelt. Grazing habits are inferred because its molars are the highest yet discovered in the whole family.

A sixth line of descent has as its surviving member the so-called "Sumatran rhinoceros," found, also, in eastern Bengal and Assam as well as on the island which has given it its name. This modern animal has small incisor tusks and a pair of relatively small but effective horns—one in the center of the nasals and a smaller behind the first and in the center of the forehead. It is a browsing forest dweller. The ancestors of this ceratorhine (the name is anglicized from the Latin name of the genus, *Ceratorhinus*) are unknown earlier than the Middle Miocene in western Europe. These earliest known forms were relatively small and slender but had increased considerably in size by the Upper Miocene. They have not been found in Asia before the late Pliocene. Although two horned, they are not related to the African two-horned species except through their remote and as yet unknown ancestry.

The seventh line of descent may be called the "rhinoceratine line," for it is the only one to which the generic name Rhinoceros is properly applied. No member of this series has ever been found anywhere outside Asia, and little is known of its more remote ancestry. It has not been found earlier than the Middle Pliocene of India, at which time it was essentially modern in its features so that no lengthy description is necessary. The top of the skull is concave because of the great amount of thickening

of the nasals to support the single massive, but short, horn. The snout was and is pointed, and incisor tusks are present. Two species survive, although they are becoming rare and the larger is approaching extinction. These two are *Rhinoceros sondaicus*, a relatively small animal, chiefly browsing in habit; and the classic and powerful *Rhinoceros unicornis* of India, which has relatively high grinding teeth and is chiefly grazing in habit.

The eighth line is called the "dicerine" (from the genus Diceros) or "atelodine" (genus Atelodus). They have two horns, tandem—one on the nasals and the second on the forehead—both are long, the first extremely so, and sharply pointed. The dicerines are otherwise distinguished from all other rhinoceros by the vestigial condition or total loss of incisor and canine teeth. Their ancestors are first known from the base of the Pliocene in Greece (*Ceratotherium pachygnathum*) and are believed to have been immigrants into that region from an African ancestral home, since they are associated with fossil remains of other animals thought to have been of African origin.

These dicerines ranged all over Europe and as far east as Persia in the person of the woolly rhinoceros of the Pleistocene (*Ceratotherium antiquitatis*). This most interesting animal was a contemporary and occasionally the prey of our own ancestors of the old stone age and is unmistakably pictured in the cave art of the Cro-Magnon human race of western Europe, and it is from the work of these prehistoric artists that we have learned much concerning the proportions, length of horns, and general hairiness of these animals. Not only did they have long hair like the hairy mammoth, but also they similarly had a woolly undercoat of brownish shade, as is learned from partially preserved specimens frozen in the Northern ice for thousands of years. This dense fur enabled it to withstand the rigors of ice-age climates and the cutting winds that swept across the steppes and tundras which bordered the ice fields. The dicerine line survives in the existing African species—the pointed-muzzled, black rhinoceros (*Diceros bicornis*) and the wide-muzzled white one (*Ceratotherium simum*), the latter the largest living rhinoceros.

The foregoing is a very much simplified account of rhinoceros history, indeed, information is lacking at many points before this history can be made complete. All mammals, especially the herbivorous kinds, tend to occupy all the various environments that are not forbidden by climate, more powerful com-

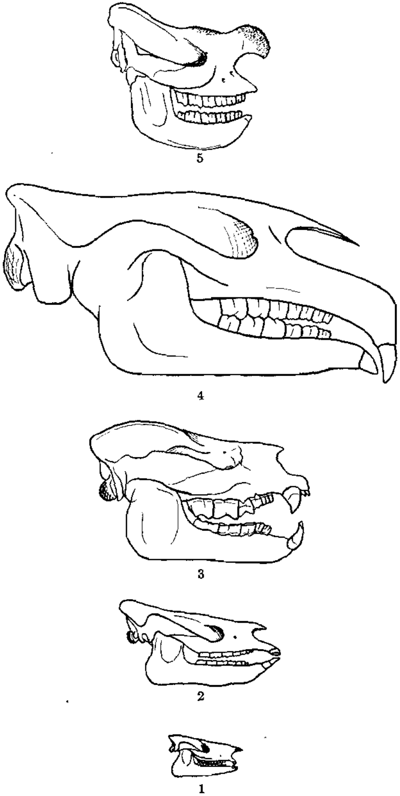

FIG. 170.—Skull adaptations in the Rhinoceros family, all about one-twentieth life size. 1. Hyrachyus. 2. Aceratherium. 3. Metamyodon. 4. Baluchitherium. 5. Ceratotherium simum.

petitors for food, or enemies too numerous to permit their permanent existence. Consequently, in the paleontological record various lines of descent are observed passing through similar adaptive stages as they became specialized for a grazing life in the more open country or a browsing one in the more forested country or sought to escape their enemies by running away or stood their ground and fought with tusks or horns. All parts of the skeleton did not progress uniformly. In one line, the skull may be progressive and the feet or the teeth conservative, or *vice versa*. Thus, the clue to true relationships in the rhinoceroses, as in all organisms, is ancestry and not similarity of adaptations. Powerfully horned forms, of necessity, had to have a more powerful mechanism behind the horns, that is to say, a shortened skull and neck and greatly modified nasal and frontal bones, or both, and larger areas for the attachment of the necessarily more powerful muscles. Hornless browsers retained the ancestral long, narrow skull.

In general, there was a gradual increase in size of body throughout rhinoceros history, although, as has been seen, the largest was not the latest, so exceptions have to be allowed for. Although the history was complicated and a geneological tree that does not contain a considerable element of conjecture cannot be drawn up at present, this fact stands out clearly—that they show a series of gradual modifications in various directions and to various degrees from a common beginning.

Order Cetacea

The order Cetacea includes the existing whales, dolphins, and porpoises as well as certain extinct related forms. Although entirely fishlike in their form and habits, they breathe air, are warm-blooded mammals suckling their young, and were evidently derived in late Cretaceous or early Eocene times from terrestrial ancestors.

They are so perfectly adapted for continuous life in the water that the early naturalists all thought that they were fishes, and the structural and physiological adjustments that have resulted in this perfect adaptation afford one of the most interesting chapters of evolution. This adaptation is so much more complete than it is in the case of the seals, for example, which we know are closely related to the terrestrial Carnivora (see table

of mammalian classification, p. 295), that we are very uncertain about the ancestry of the whales.

Suborder Zeuglodontia.—The Zeuglodontia or Archæoceti comprise the oldest known whales. Of the nine genera which have been discovered the earliest (Pappocetus) is from the Lower Eocene of Africa. Four additional genera make their appearance in the record in the Middle Eocene, and one of these is the genus Zeuglodon, or Basilosaurus, as it is more correctly called, and which becomes world wide in its range in the Upper Eocene. At this time, two additional genera (Dorudon and Zygorhiza) are introduced, and two additional genera (Kekenodon and Phococetus) are known from only the Upper Oligocene; these last represent the latest known members of the suborder.

Although but a few representatives of this primitive group are thoroughly known, they illustrate the gradual reduction of the hind limbs, the shortening of the neck, and many changes in the teeth, such as an increase in size of the incisors and a reduction in size of the molars with the loss of the last upper one.

The bones of the skull were of the normal mammalian number, form, and relationships; the face was elongated; and the cranium was narrow and unshortened. Their ancestors among terrestrial mammals are uncertain, but the relatively small Protocetus of the Middle Eocene of northern Africa has a dentition almost exactly like those found in the Eocene terrestrial mammals known as "creodonts."

The Upper Eocene Zeuglodonts reached a length of 50 to 70 feet but remained relatively slender and swam in a serpentine manner, as is indicated by the structure of the vertebræ. On the contrary, the two known Oligocene genera were much smaller, relatively shorter, and their structure indicates that they swam in the same manner as the living whales, that is, by means of tail flukes.

Suborder Odontoceti.—The Odontoceti or Denticeti comprise the toothed whales—the prefix *odonto* in the first name being derived from the Greek, and *denti* in the second name being derived from the Latin "toothed." They make their first appearance in the Upper Eocene of North America in the genera Archæodelphis, Agorophius, and Xenorophus. Several additional genera make their appearance during the Oligocene.

The suborder comprises eight families and over one hundred genera and includes the extinct squalodonts, the existing sperm

and beaked whales, the belugas, narwhals, dolphins, porpoises, as well as the river dolphins of southern Asia and South America. During their history, the Odontoceti show a progressive shorten-

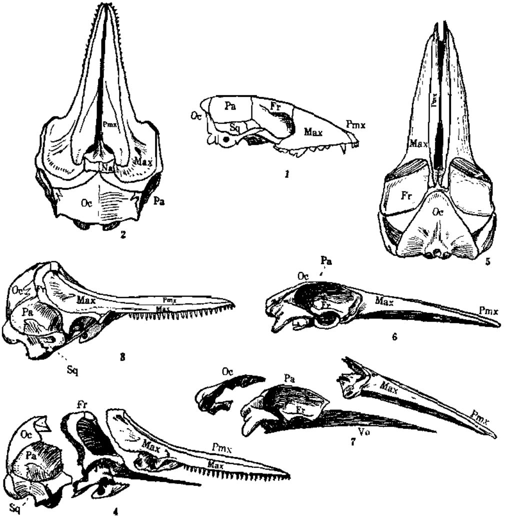

FIG. 171.—Showing the modification of the skull in the toothed and whale-bone whales. 1. Side view of a skull of a jackal in the Johns Hopkins University collections, showing the normal arrangement of the principal cranial bones in a *terrestrial mammal, all much reduced.* 2. *Top view of the skull of a bottle-*nosed dolphin, Tursiops. 3. Side view of the same. 4. Side view with the bones disarticulated to show the manner in which they are slid over one another, especially the maxillary over the frontal. 5. Top view of the skull of a rorqual, Balænoptera. 6. Side view of same. 7. Side view with the bones disarticulated to show the way the forked maxillary is arrested by the frontal and the manner in which the occipital has slid over the parietal and frontal. (*Figs.* 2–7 *after Kellogg.*)

ing of the cranium, which is mainly accomplished by the overlapping backward of the maxillaries over the frontals until they nearly or quite meet the supraoccipital at a level behind the orbits. The maxillaries also widen behind, thus almost covering the frontals and pushing the parietals from their median position

between the frontals and occipital to the sides of the skull. In Figure 171,[1] the normal arrangement of the bones concerned is shown as they occur in a terrestrial mammal, and their modified arrangement as seen in the existing bottle-nosed dolphin (Tursiops) is shown in Figs. 171,[2] 171[3], and 171.[4]

Suborder Mysticeti.—The whalebone whales comprise three families and about thirty-six genera. They are found, first, in the Oligocene (Pachycetus), have seven living genera, and a considerable number of incompletely known fossil species. The Mysticeti show the same progressive shortening of the cranium as do the Odontoceti, but in the former this shortening and widening is accomplished, in large part, by the forward elongation of the supraoccipital and parietals over the frontals, the maxillaries being seemingly held by the supraorbital processes of the frontals so that the posterior border of each maxillary is forked.

The whalebone whales are obviously derived from toothed ancestors, as is indicated by the presence of numerous teeth in their embryos. These embryonic teeth are resorbed during development and are replaced by the strainer-like plates of whalebone, just as their ancestors became toothless by becoming adapted to a diet of small pelagic crustaceans and fishes, which required no mastication but simply an apparatus for catching them in large quantities. How admirably the plates of whalebone with their fibrous inner margins perform the function of a huge strainer is indicated by a statement of Andrews that four barrels of shrimps were taken from the partially filled stomach of a blue whale whose throat was only about 9 inches in diameter.

This peculiar habit of taking food has profoundly influenced the proportions and structure of the skull. In the large Basilosaurus of the Upper Eocene (Suborder Zeuglodontia), the skull is about one-twelfth the total length of the body. In some whalebone whales, it may be one-third the total length, and the head proportion varies in different existing species from one-third to one-sixth the total length. This, too, in a group which contains by far the largest known warm-blooded animals the world has ever known. The accompanying figure of the skull of a young Rorqual (Balænoptera) shows the peculiar modifications in this suborder (Figs. 171[5], 171[6], and 171[7]).

Some Evolutionary Trends.—The more general oceanic adaptations among the whales illustrate the same principles as

were illustrated by the ichthyosaurs and, to a lesser degree, by the other less completely marine reptiles of the Mesozoic era, or by such mammals as seals.

These comprise the assumption of a fishlike body form, with the elimination or burial in the flesh of all protruding parts which might offer resistance to a rapid movement through the water; the loss of external hind limbs, and the transformation of the forelimbs into flippers for steering and balancing; the development of a tail fin (caudal flukes) as the sole organ of propulsion, whereas in the first whales the limbs must have furnished the motive power. Secondary changes accompanying the foregoing were changes in the form of the vertebræ, the shortening of the neck, the fusion of the wrist bones, and the multiplication of the finger bones.

More special modifications were the remodeling of the skull bones in the Odontoceti and Mysticeti, which were brought about by the slipping of some of the cranial bones over others ("telescoping") and the reduction of some and the enlargement of others, thus virtually effecting a rearrangement of the bones in so far as their contact relationships are concerned. This resulted in a shortening and widening of the cranium and the practical elimination of the intertemporal region of the skull.

Other adaptations, which may be called "physiological," are the layer of blubber covering the body which insulates it and conserves the body temperature against the conductivity of the water, which is so much greater than that of the air; the internal adjustments for maintaining a supply of oxygen for the tissues and disposing of some of the accumulating carbon dioxide so that whales can remain submerged. This submergence is normally for periods of from 5 to 15 minutes, but it may be prolonged for as much as 2 hours if the necessity arises.

Other adaptations are devised for preventing water from getting into the lungs. This is accomplished by having the external opening of the nostrils—single in the Odontoceti and double in the Mysticeti—not connected with the throat as it is in land mammals but directly connected with the windpipe and, also, provided with an automatic closing device which differs in its details in the two suborders. The eyes are modified to resist pressure and to prevent any irritation by constant submergence in salt water and to receive as much dispersed light as possible. Whales do not see very well, however, and brain casts

that have been made of some of the fossil forms show a progressive disuse of the eyes during their geologic history. The sense of smell is practically gone in modern whales, and there has been a very great modification of the organs of hearing—the last the most used sense in existing whales. The external ears are gone, and the external opening is extremely minute. The essential organs of hearing are deeply buried, much modified, and the principle of resonance is utilized for magnifying the sound waves received through the water.

Ancestry.—Little of a definite nature can be said of the ancestry of the whales. Expert opinion is agreed that the three suborders do not go back to a single common ancestor, but this does not mean that their remarkable similarities have been attained from unrelated ancestors. Rather, we may consider the terrestrial ancestors of the three suborders to have been closely related and to have differed merely in certain minor structural features, such, for example, as the nature of the sutures between some of the cranial bones.

That the ancestors of the Cetacea were terrestrial mammals is indicated by their common ground plan of structure and function, by the vestiges of hind limbs, by embryological evidence, and by the traces of a coat of fur in some of their newly born babies.

Order Primates

The order Primates, which includes the lemurs, monkeys, apes, and man, was so named by Linnæus from the Latin *primus*, meaning "first."

Definition.—Plantigrade mammals with five fingers on each hand and five toes on each foot, with broad, flattened nails (occasionally one or more may be clawlike). The tooth formula, easily derived from the primitive mammalian, is generally $i\,\frac{2}{2}$, $c\,\frac{1}{1}$, $pm\,\frac{2}{2}$, $m\,\frac{3}{3}$. All except the molars are preceded by milk teeth. The molars are three, four, or five cusped. Clavicles or collar bones are present in the shoulder girdles. Orbits are surrounded by bone and are directed more or less forward instead of laterally. The stomach is simple, and the milk glands are usually two in number and situated on the chest. As a rule, but a single offspring is produced at birth, and the young are born in a completely helpless condition. The diet is chiefly or wholly vegetable and the habits chiefly or wholly arboreal,

with the exception of man. The limbs are prehensile and a more or less opposable thumb and great toe are present. The Primates are dwellers in warm climates, except in the case of man who has risen superior to climate by his cleverness, and the existing Primates, other than man, are the modified survivors of the prehuman stages in the evolution of man, adapted in different directions.

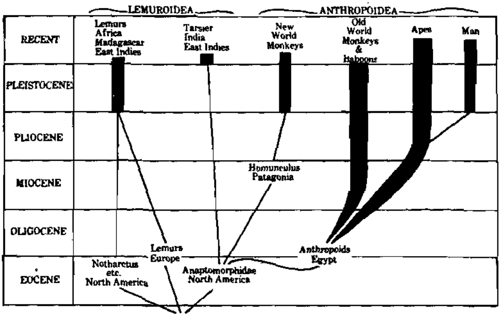

FIG. 172.—The relationships and the known geological history of the Primates. (*Modified from Matthew.*)

The Primates are capable of segregation into two suborders—the Lemuroidea or Prosimiæ, and the Anthropoidea or Simiæ and their mutual relations and known geological range are shown in the accompanying diagram (Fig. 172).

Suborder Lemuroidea.—At the present time the lemuroids are confined to the warmer parts of the Old World (see distribution map, Fig. 173). They are small, arboreal, quadrupedal, and mostly nocturnal animals, with a generally long and hairy tail which is not prehensile. The second toe has its nail modified into a claw. The orbits are not completely closed off from the temporal region by bone. Being nocturnal in habits, their eyes are large, which give them a somewhat peculiar appearance, and their relatively small brain case results in their having a protruding, foxlike face.

There is quite a variety of existing species, chiefly in Madagascar, and fossil forms have been discovered in the earlier Tertiary of western North America and Europe. As a group they are undoubtedly derived from some unknown, Upper Cretaceous, progressively brained, arboreal Insectivora. They are divided by Gregory into three series, with seven families in all. They are rare as fossils and after the early Tertiary (genera Notharctus, Pelycodus, Telmalestes, Protoadapis, Pronycticebus, Nectrolemur, etc.) disappear from the geological record in

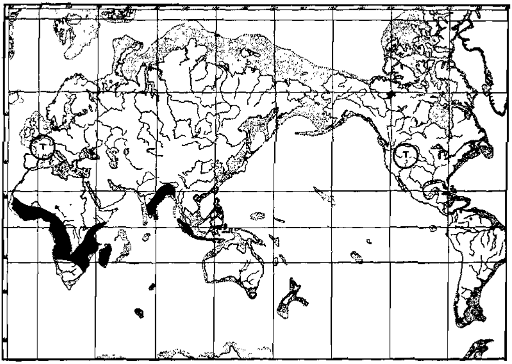

FIG. 173.—The present distribution of the Lemuroidea and the location where early Tertiary fossil forms have been found, indicated by *T*.

North America and Europe. Much more modern in structure are those found fossil in comparatively recent deposits in Madagascar (Nesopithecus and the relatively large Megaladapis).

Suborder Anthropoidea.—In this suborder the cranial capacity is relatively much more than in the Lemuroidea, the cerebrum completely covering the cerebellum in all except a few American monkeys. The canine teeth are enlarged (except in all men but the Piltdown, Eoanthropus). All of the Old World forms, including man, have an identical dental formula of $i\ \frac{2}{2}$, $c\ \frac{1}{1}$, $pm\ \frac{2}{2}$, $m\ \frac{3}{3}$, but the American family Cebidæ have an extra premolar, $pm\ \frac{3}{3}$, and the American marmosets or squirrel monkeys have a formula

i $\frac{2}{2}$, *c* $\frac{1}{1}$, *pm* $\frac{3}{3}$, *m* $\frac{2}{2}$, having the extra premolars of the Cebidæ, and having lost a pair of molars from each jaw.

The great differences in the appearance of the different anthropoids is due to their relative proportions brought about by their various habits of life. The anthropoids fall naturally into two great series—a New World and an Old World series—which represent lines of evolution that have probably been independent since the early Tertiary. The distribution of the existing anthropoids, other than man, and the location and age of fossil forms are shown in Fig. 174.

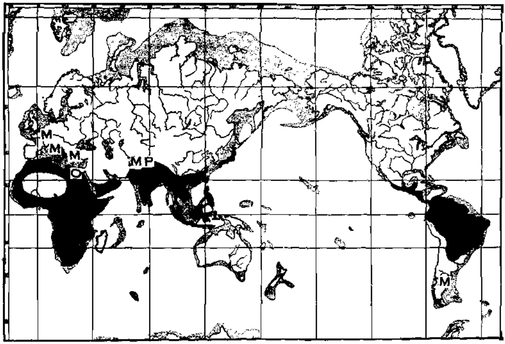

FIG. 174.—The present distribution of the monkeys, apes, and baboons, that is, the Anthropoidea other than man, and the known fossil occurrences. *O*, *Oligocene*; *M*, *Miocene*; *P*, *Pliocene*.

The American monkeys are termed the Platyrrhina, from the Greek for "broad nosed," a feature due to the wide, bony septum between the nostrils. They comprise the two families Cebidæ and Hapalidæ, the members of both being highly specialized for an arboreal life, and they are remote from the ancestry of man. They are, therefore, much less interesting than the Old World forms. Among the adaptations in the American monkeys are the greatly reduced thumbs and the long, prehensile tails of the spider monkeys (Ateles) and the squirrel-like size and shape of the marmosets, in which all of the nails except those of the first toes have become clawlike.

Fossil forms of several platyrrhine monkeys have been found in Pleistocene cave deposits in South America (representatives of the genera Cebus, the Capuchins; Mycetes, the howlers; and Callithrix, the titi), but these shed no particular light on their geological history. The only more ancient record is Homunculus from the late Miocene or early Pliocene of Patagonia, incompletely known but thought to be a possibly intermediate stage between certain North American Eocene lemuroids and the platyrrhine series.

The second or catarrhine series, which includes the Old World monkeys, baboons, apes, and man, gets its name from the Greek for "narrow nose," due to the thin nasal septum. The Catarrhina are a much more extensive group with more numerous fossil forms than the preceding. They are commonly considered to be made up of the four families Parapithecidæ, Cercopithecidæ, Simiidæ, and Hominidæ.

The Parapithecidæ comprise several genera (Parapithecus, Propliopithecus, Moeripithecus, and Apidium) found in the Lower Oligocene of Egypt and representing the earliest known anthropoids. They were small animals, distinctly primitive, but with the fundamental molar and premolar patterns of their successors. Propliopithecus, in particular, foreshadows the later genera Dryopithecus and Pliopithecus and may have also been a collateral ancestor of the Cercopithecidæ.

The second family—the Cercopithecidæ—comprise the Macaques, baboons, and langurs and exhibit a great variety of proportions and secondary modifications. Thus, there are hairless callosities on the rump, the tail is never prehensile, a vermiform appendix is wanting, and the baboons are largely terrestrial in habit with elongated muzzles and powerful canines. Fossil members of this family are rare but include the extinct genera Oreopithecus of the European Miocene (representing a distinct subfamily) and Mesopithecus and Dolichopithecus in the Pliocene of Europe. In addition, the existing genus Macacus (macaque) is represented in the Pliocene and Pleistocene in Europe, Asia, and northern Africa: the genus Papio (baboon) is present in the Pliocene and Pleistocene of India and the Pleistocene of northern Africa: and Semnopithecus (langur) occurs in the Pliocene of Europe and Asia.

The third family—the Simiidæ—is of more immediate interest, since it includes man's nearest living relatives, and its separation

from the family Hominidæ is, to a large extent, a matter of sentiment rather than of zoological evidence. Except that one genus (Hylobates, the gibbons) has a callosity on the rump similar to that of the Cercopithecidæ; that the arms are relatively long and the legs short; that the big toe is habitually opposable; the Simiidæ are structurally like the Hominidæ, and many scientists think that both the apes and man should be grouped together in a single zoological family.

Since a discussion of the relationship of the great apes as well as their fragmentary fossil remains would be lengthy and highly technical, only a table of the existing and extinct genera will be given, and such remarks as are appropriate will be found in the discussion of the ancestry of man, which follows.

Family Simiidæ (Apes)

	Home	Fossil occurrence
Existing genera:		
Simia- orang utan	Sumatra and Borneo	Pliocene of India
Pan (Anthropopithecus)-Chimpanzee	Equatorial Africa	None known
Gorilla (Pan)-gorilla	Tropical West Africa	None known
Hylobates-gibbon	Asia, Assam, and Burma to Hainan and Cambodia	None known
Extinct genera:		
Australopithecus, the man ape of the later Tertiary of South Africa		
Pliopithecus, ancestor of the gibbon. Upper Miocene and Lower Pliocene of Europe		
Dryopithecus, ancestor of man, gorilla, and chimpanzee. Upper Miocene and Lower Pliocene of Europe and Asia		
Palæosimia, ancestor of the orang. Upper Miocene of India		
Sivapithecus, intermediate between Dryopithecus and Palæosimia. Upper Miocene of India		
Palæopithecus, ancestor of gorilla. Pliocene of India		
Neopithecus (Anthropodus). Pliocene of India		

The family Hominidæ (man), as already stated, is a largely psychological group, including all of the existing races of man, which are, by convention, referred to the single species *Homo sapiens*. The genus Homo is known as far back as the first or second interglacial period (there being differences of opinion

as to which of these horizons contains the Heidelberg man) and is represented by at least two extinct species—the Heidelberg man, *Homo heidelbergensis;* and the Neanderthal man, *Homo neanderthalensis.* There are, in addition, at least three extinct genera—the ape man of Java, *Pithecanthropus erectus;* the Piltdown or dawn man of England, *Eoanthropus dawsoni;* and Sinanthropus from the Lower Pleistocene of China.

Morphology, embryology, and physiology indicate that the existing apes, despite their marked specializations, are man's nearest living relatives and are less removed from their common ancestry than is man himself. All fossil primates known, as well as the development and structure of the human foot, show the indelible impress of arboreal adaptations and set apart the Primates from all terrestrial quadrupedal mammals, although some authorities dispute these conclusions.

Man differs from the rest of the anthropoids chiefly in his long legs, short arms, progressive thumb, and foot adapted for terrestrial life with the loss of opposibility of the great toes; but the structure of hand and foot, the ground plan of molar-tooth pattern, and the nervous, visceral, and skeletal adjustments of his body are a heritage from apelike ancestors. The skull shape in man is caused by the enlarged brain and a shortening of the face due to the lack of prominence of the canine teeth, which are tending to become like incisors, and, because they no longer project as in apes (except in the Piltdown man), the tooth series is continuous, that is, without spaces in front of the upper canines and behind the lower canines for their overlapping tips.

This shortening of the jaws also results in the teeth's being in a more perfectly arched series. The reduction in the jaws, due to food habits, was accompanied by a corresponding reduction in size and power of the muscles, with a corresponding change in the form of the head and neck. All of these characters, and others which might be mentioned, which are used to separate the Hominidæ from the Simiidæ, are relative and adaptive and of slight zoological importance.

Fossil remains of all of the primates are rare, chiefly because they were primarily forest dwellers where bones quickly decay, and because their bones are relatively fragile. The wonderful panorama of Tertiary animal life found in Patagonia need but be contrasted with that of Brazil or that of our Western with our Eastern states to show how much more favorable for fossili-

zation are the open country plains regions as compared with those that are forested. Fossil remains of man are especially rare, and the surprising thing is not that they are not more common but that so many should be known and now that a knowledge of their importance is becoming general, new discoveries are turning up almost every year.

It may properly be inferred that the long apprenticeship in the trees of man's ancestors was an important factor in the development of brain power. Thus, the gibbons which are the smallest and most monkey-like of the apes—so much so that some authorities would associate them with the monkeys rather than with the apes—have a smooth cranium and short face with the head poised in a quite human way. At rest they habitually sit with the arms and hands free, and on the ground they walk erect but, of course, very clumsily. In the trees they are among the most acrobatic of anthropoids, the hands and arms being the sole organs of locomotion. Such a mode of progression requires the greatest precision in the perception of direction, distance, and strength of branch, and that it has an educational value is shown by the relative great development of the centers of sight, touch, and hearing in the gibbon's brain.

The author does not mean to suggest that the gibbons belong to the human genealogy—they are remote from it—but they illustrate the premium which nature places on intelligence and the sort of school in which it is developed. Man was not possible until the hands had been freed to become the tools of the brain.

The oldest human fossil—the ape man of Java—was a forest dweller that had drifted southeastward down the great river valleys of southeastern Asia along with the other forest life as the late Tertiary changes of topography and, consequently, of climate, were replacing the forests of central Asia by a progressively more open type of country. This change from forested to open country is believed to have been one of the principal factors in the adoption of a terrestrial mode of life. Of course, these early forms did not pass rapidly from arboreal to terrestrial habits but gradually and by a series of slow stages during which they were semiarboreal or semiterrestrial, like the present-day great apes.

Terrestrial life, without an easy refuge from enemies by retreat to the trees, was a tremendous stimulus to thinking and planning or, perhaps it should be called, choice and cunning. The survival

premium was placed on brains. That this is not merely theory is shown by the contrasts between forest- and plains-dwelling human races in the modern world, and an actual fossil example is furnished by the much disputed skull of Australopithecus, discovered recently by Dart in South Africa. This skull is of an immature individual of uncertain geological age but probably as ancient as pre-Pleistocene, which lived in a practically treeless country. Australopithecus was an undoubted ape and resembled a modern chimpanzee, but its brain was most progressive in size and structure, if we may properly judge from a single immature specimen. This progressiveness is fairly to be correlated with the demands of an open-country mode of life.

Darwin and some later scientists have regarded Africa as the real birthplace of man. One anthropologist argues for western Europe, but the majority favor Asia for reasons that may well be regarded as conclusive—its size and central position, the seemingly suitable physiographic and climatic changes that are known to mark its late Tertiary history, the fact that it was the center of radiation of other mammalian lines, and the fact that the great apes and the most primitive modern races and fossil men (Pithecanthropus) have a similar distribution southward from this supposed ancestral Asiatic home and correlated with the above-mentioned physical changes.

All of the living apes have a largely frugivorous diet, which means that in an animal of any size, much of their time is taker with procuring food, and if they are both large and active th amount of food required is greatly increased. Thus, the existin great apes, especially the orang, are all sluggish animals and therefore, would stand but a slight chance of permanent surviva under completely terrestrial conditions.

Terrestrial life, in man's remote ancestors, was a constar stimulus to new sorts of food—insects, birds, roots, stream lif and, doubtless, carrion of all kinds. As soon as these prehuma beings achieved intelligence enough to use sticks and stones weapons they would greatly expand their bill of fare. Anim food is much more concentrated than vegetable, and a large carnivorous diet once acquired would allow time for other thin this, also, was one of the greatest factors in subsequent progre

At first, the most primitive weapon was a stick. Later, th were more and more fashioned, but we can scarcely hope ever find an actual specimen, for wood usually decays rapidly, a

if we had found fossil sticks in the same strata with the ape man, how could we recognize that they were weapons and not just chance sticks? Another primitive weapon was a stone of suitable size for throwing at some object or for pounding open oysters or clams or cracking a bone for the marrow or breaking a stick to the hand. Suitably sized and shaped stones were doubtless cherished, and it is but a step from selected stones to attempts at fashioning them in a rude sort of way to knock an edge or a point on one by hitting it with another.

These earliest weapons or tools of stone are difficult to distinguish, as identical chipping occurs naturally through interaction of adjacent stones in a gravel under pressure or any natural causes that induce movement—the pounding of shingle by waves, violent steam action, or sudden, natural changes of temperature. Stones, usually of flint, which show rude traces of fashioning, are called "eoliths," and such are found at various ancient horizons, but the author knows of no way of distinguishing between natural and artificial eoliths, since both depend on the natural fracturing properties of the stone. The eoliths of the late Pliocene of eastern England are proved to be artificial by the circumstantial evidence of their occurrence in certain layers, their age, and the evidence of fire associated with them. If similar stones are found in the Eocene they become absurd as evidence of human industry. We may, therefore, admit the existence of an eolithic stage of human industry antedating the time when certainly recognizable stone weapons and tools were fashioned systematically to certain definite shapes, but we must recognize that very similar objects due to natural causes occur at many geological horizons and wholly lack any human implications.

Artificial weapons or tools are known as "artifacts" and are as truly human fossils as are human bones, for fossils are not only the actual remains of organisms preserved in the rocks but also any traces of organisms, so that it is quite as correct to speak of an anciently buried stone arrow point as a "fossil" as it is in the case of the footprint of a Triassic dinosaur or the trail of a Cambrian worm.

Much that is known of the earlier stages of human progress depends upon these artifacts, for they are always more abundant and widespread than the bones of their users. Authorities differ very greatly in their estimates of the relative ages of some of

these fossil relics of man, because often the evidence is insufficient. Most glacial and interglacial deposits are much alike, so that unless there is evident the whole sequence of horizons, much remains doubtful. Then, too, human races and human industry represented by flint weapons and tools became modified more rapidly in some regions than in others and spread with inconceivable slowness, so that there was much overlapping in time. Asia was generally hundreds of years in advance of Europe. Thus, even as late as the bronze age or early iron age (Hallstatt), these metals were in use in Asia 800 to 1,000 years before their use became at all common in Europe.

Old and rude types of flints like the scarcely retouched eoliths are often found associated with later types, just as the American Indians were in the stone age of culture at the time of Columbus and long afterward, even though in Mexico and Peru certain metals were worked.

The time table for human paleontology adopted here is given on an adjoining page, and this applies only to western Europe, which is the only region where anything like the complete sequence is known. Such outlying finds as the Rhodesian skull cannot be dated. Nor have any satisfactory conclusions been reached as to the time of arrival of early man in North America. It is only fair to say that the differences of interpretation mentioned have to do with such questions as whether the Heidelberg bones are older than those from Piltdown and whether the first or second interglacial is the proper horizon and do not in any *way affect the truth of man's antiquity and evolution.*

The oldest definitely placed human remains come from the island of Java and date from the early Pleistocene. Evidences of human industry in the form of the rudely chipped flints occur still earlier, but our information regarding the ape man of Java—*Pithecanthropus erectus*—the so-called "Trinil race," is on a much sounder footing.

In 1891, E. Dubois discovered the top of a skull, a left thigh bone, and two teeth in a river-terrace deposit near the village of Trinil, on the Solo River in the island of Java. The next year another tooth was found. A German expedition to Trinil in 1907–1908 failed to find additional human bones but collected many other fossils, both animal and plant, which proved that Pithecanthropus was early Pleistocene instead of Pliocene, as Dubois had supposed. The inside of the skull cap was cleaned,

and casts made of the brain cavity, and this and the precious relics of bone have been searchingly studied by many scientists.

TIMETABLE OF PREHISTORIC HUMAN HISTORY

Geological divisions	Culture stages			Human bones
Post glacial	Iron age { La Tène, Hallstatt			
	Bronze age			
	Neolithic	*Carnacian, dolmens*		
		Robenhausian, *pile houses*		Lake dwellers
		Campignian, pottery		
		Maglemosean, kitchen middens		
		Azilian-Tardenoisian, painted pebbles		Grenelle-Furfooz
Fourth glaciation (Wurm, Mecklenburgian, or Wisconsin)	Paleolithic	Magdalenian, art and bone objects	Capsian in North Africa and Spain	Cro-Magnon
		Solutrean, leaf points		Cro-Magnon { Brüx, Brünn, Predmost
		Aurignacian		Cro-Magnon-Grimaldi
		Mousterian		Neanderthal
Third interglacial (Neudeckian or Sangamon)		Mousterian		Neanderthal
Third glaciation (Riss, Polandian, or Illinoian)		Mousterian Acheulean		Neanderthal-Weimar Krapina
Second interglacial (Helvetian or Yarmouth)		Chellean		
		Pre-Chellean		Piltdown
Second glaciation (Mindel, Saxonian, or Kansan)		Pre-Chellean		
First interglacial (Norfolkian or Aftonian)		Pre-Chellean		Heidelberg
First glaciation (Gunz, Scanian, or Nebraskan)		Pre-Chellean		Trinil
Preglacial	Eolithic	Foxhallian		

The skull was long and narrow—a human and non-ape character. It was also low, and the brain mass has been variously estimated between 850 and 950 cubic centimeters, as compared with 650 of a modern gorilla with twice the body weight of a man. The Trinil brain was primitive but essentially human in the important frontal and temporal regions, although these were

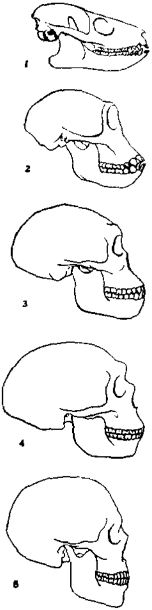

FIG. 175.—Showing various Primate skulls in outline (not drawn to scale). 1. Primitive Primate of the Eocene, *Notharctus*. (*After Gregory.*) 2. Chimpanzee. (*After Gregory.*) 3. The ape man, Pithecanthropus. (*After McGregor.*) 4. The Neanderthal man, *Homo neanderthalensis*. (*After Boule.*) 5. Modern man, *Homo sapiens*. (*After Gregory.*)

much less developed than in later races. The region of the motor-speech center and the so-called "auditory-speech" center indicate, in the opinion of the foremost authorities, that Pithecanthropus had already acquired the power of speech. The shape of the thigh bone proves him to have been an erect terrestrial biped and not arboreal. If the proportions were those of modern man, which is doubtful, he would have been about 5 feet 8 inches tall and would have weighed about 155 pounds.

The details regarding these Trinil bones are highly technical. Opinions differ regarding the exact status of Pithecanthropus in the human geneological tree. Some authorities (Keith) would refer him to the genus Homo and consider him in the direct ancestral line, but most students regard him as only a collateral ancestor. The animals and plants found fossil with Pithecanthropus include some 15 species of mollusks, several fishes, a gavial, crocodile, 5 turtles, several birds, over a score of mammals, and 54 species of plants. These last indicate an evergreen, rain forest country with a slightly lower temperature and a greater rainfall than at the present time in Java. The ancestors of these animals are found in the Pliocene of northern India, and the plants are like those found in Assam. This proves the more northern origin of the Trinil assemblage and stamps the ape man as a backward, forest-dwelling type, removed from competition with the progressive human types that we assume existed in those early days on the plains of central Asia.

The next younger traces of human bones take us to a complete lower jaw, found 79 feet below the surface in a sand pit at Mauer,

near Heidelberg, Germany, in 1907, and supposed to have been buried by natural processes during the first interglacial period. This jaw has been christened *Homo heidelbergensis* and is frequently referred to as the Heidelberg man or even race, although the single jaw was its sole representative until a few years ago when parts of the leg and foot bones were discovered. The jaw is very massive, with a receding chin (an ape feature) but thoroughly human teeth. In its details it much resembles the jaw of a modern orang. The molars have short, divergent roots, and all except the left hindermost have five cusps. We can get an idea of the whole head from the muscles necessary to operate such a jaw and from similarities to the later and better-known Neanderthal skulls.

The associated flints are very crude, and these, together with the associated mammal bones, indicate an early Pleistocene age. After this time, flints of the primitive pre-Chellean type are found in deposits of the time marked by the waxing and waning of the ice sheets of the second glaciation and amounting to a good many thousands of years before any additional human bones were discovered.

The next bones belong to the so-called "dawn man" of Sussex, England, *Eoanthropus dawsoni*, discovered in 1911. These include fragments of a skull, three teeth, and a portion of a jaw, and subsequent patient and thorough search have been rewarded by additional skull fragments and another tooth. The Piltdown man, as these have been called, probably lived during the long and warm second interglacial period. With him were found the pre-Chellean type of flints. The skull lacks the primitive bony ridges over the eyes and the low, sloping forehead of the much younger Neanderthal race of the third interglacial. The walls of the cranium are tremendously thick and the brain relatively small, around 1,300 cubic centimeters, with rather undeveloped speech centers. The jaws were protruding, and although the molar teeth are human, the canines project much like those of a chimpanzee, and some students have held that the jaw does not belong with the skull but represents an extinct species of chimpanzee. Opinion on this point has fluctuated but is now in favor of the view that the skull and jaw belong together.

The Piltdown man is the third and last representative of what have been called the "river-drift men" who lived in the open and whose remains have been found in river deposits formed

under mild climatic conditions. One reason why their remains are so rare is because, in addition to the frailty of human bones, their dead were either left for beasts of prey to consume or, if buried, were placed in the ground where they soon decayed.

A long time interval now ensued during which the flint weapons that have been found show an advance in workmanship and are of a type known as Chellean. It is not until the close of the third glaciation that additional human bones were found, and then they occur in some abundance because they belong to a race of cave dwellers, inhabitants of caves in the limestone regions of Europe, where the chances for preservation are much better than in the case of the river-drift men.

This oldest known race of cave dwellers is called the Neanderthal race. It made its appearance in western Europe during the third glaciation and lived on there for a longer period than have the Anglo-Saxons, disappearing in the early stages of the fourth glaciation. Over a period so long and an area so extensive the skulls show some variation, and it is customary to distinguish the earliest or Krapina men, which some anthropologists believe to have been associated with the Acheulean weapons, from the later remains associated with Mousterian culture characterized by flints which are usually chipped upon but one side.

Early occurrences of Neanderthaloid bones are found at Krapina (northern Croatia), Taubach and Ehringsdorf (near Weimar, in Germany), and Le Moustier (France). Middle Mousterian bones have been found at four different localities, including the nearly complete skeleton of La Chapelle-aux-Saints near Brive in France. Late Mousterian bones have been discovered at six different localities, and there are nine different localities—eight in Europe and one in Palestine—where Neanderthal bones have been discovered but where the exact horizon cannot be determined. These last include the Gibraltar skull and the type of the race from Neander in Rhenish Prussia. Possibly the Rhodesian man discovered recently in South Africa should be added, for it is Neanderthaloid in many of its features.

Mousterian flints have been found at a large number of stations in Europe and recently in Mongolia, so that it is eminently proper to speak of these Mousterian men as a "race." This is important, since hostile critics have frequently been satirical over the incompleteness of the skeleton from Neander which first came before the Public.

The Krapina bones occur in a limestone rock shelter near the village of Krapina in northern Croatia and were discovered in 1899. The human bones to the number of some 300 fragments were associated with thousands of broken animal bones, which has made it difficult to get a correct notion of the complete features. The skulls are of men, women, and children and are slightly broader than the later ones, with less prominent eyebrow ridges and not quite such massive jaws, but there is the same retreating chin and flat crown. The remains from Taubach and Ehringsdorf near Weimar are of about the same age as Krapina.

The history of the discovery of Neanderthal man may now be sketched and his general make-up and mode of life briefly described. The earliest find was a female skull in a cave at Gibraltar in 1848, the significance of which was not realized until 1887. In 1856, some workmen came across a skeleton in a small limestone cave in the Neander Valley near Düsseldorf. This was probably complete when found but suffered the fate of so many similar finds whose priceless value is not realized by their discoverers. All that was rescued for science of the Neander skeleton was the skull cap, several leg bones, half of the pelvis, a fragment of the shoulder blade, and pieces of five ribs.

The celebrated German pathologist Virchow pronounced the unusual features of the Neander bones as due to disease in some modern man, and their real importance was not fully realized until 1887 when two nearly complete skeletons of the same type were discovered in a cave at Spy, near Dinant in Belgium, since which time nearly a score of skeletons has been discovered in different places, including the old man of La Chapelle-aux-Saints, in which the skull is complete except for the loss of most of the teeth.

In many of their skeletal features the Neanderthalers, variously called *Homo neanderthalensis*, *Homo primigenius*, and *Homo mousteriensis*, were more apelike than human, but their teeth were typically human and they possessed the power of speech, fashioned skins and weapons, were skilled in the use of fire and in hunting, and practiced ceremonial burial, placing implements and weapons with their dead—the first appearance in the geological record of a belief in a future life.

They were short and thickset. The tallest skeleton indicates a height of not over 5½ feet. They were very muscular, with big hands, short fingers, and a clumsy thumb. They must have

been clumsy on foot, with apelike legs, in that the shin was relatively short and the thigh relatively long. The forearm was relatively short like those of the modern Eskimos, Lapps, and Bushmen. Their arms were but 68 per cent the length of their legs, which is the reverse of the condition in the apes—the chimpanzee, for example, has an arm longer (104 per cent) than its leg.

The position of the foramen magnum (the hole in the base of the skull for the passage of the spinal column) and the character of the neck vertebræ indicate that the head was held well forward and the shoulders were stooped; the spinal column was curved like that of a modern baby and unlike that of an adult *Homo sapiens*. The head was massive, with deep face, retreating forehead, heavy, overchanging brows, broad and rather flat nose, long upper lip, projecting jaws, and retreating chin. The skull was thick but capacious and different in proportions from that of a modern man, flatter on top and projecting behind.

The brain capacity as estimated in different specimens ranges from 1,300 to 1,700 cubic centimeters, so that in size it was typically human. Its proportions were, however, decidedly different from modern man's and those parts which are concerned with the higher faculties were less developed. This is not inference but is based on careful studies of casts of the brain cavity; we even know that they were right handed.

Whether the Neanderthal race was wiped out by disease or conquest or lingered on for a long time in greatly diminished numbers is not known, but while the ice sheet of the fourth glaciation still covered northern Europe, Neanderthal men were largely superceded by the arrival in western Europe of a new race supposed to have come from Asia, a race as interesting as any race the world has known and believed by all students to belong to the same species—*Homo sapiens*—as ourselves. This race is called the Cro-Magnon and appears to have invaded Europe from Asia Minor and from northern Africa, as well.

They were skilful hunters and followed in the wake of their game animals—the wild ass, steppe horse, and various other Asiatic immigrants. Most of the sites where their remains have been found are caves or rock shelters, but several open camp sites have been discovered. Although the ice sheet of the fourth glaciation was to linger on to the northward for many thousands of years, the climate was dryer, with severe winters but fairly mild summers.

The Cro-Magnons were tall, averaging slightly over 6 feet, with large chest, relatively long legs and long forearms and shins, wide, short faces, prominent cheek bones, narrow and pointed chins, narrow and long skulls, shallow orbits, and aquiline noses. They were vigorous and fleet of foot, practiced ceremonial burial, and had much improved implements including bow and arrows and stone lamps. Their brain capacity ranged from 1,500 to 1,880 cubic centimeters, and their brains were essentially modern.

They endured with changes in weapons and art during what are called the Aurignacian, Solutrean, and Magdalenian culture stages in western Europe or what is called Capsian in Spain and Tunis. They have been called the "Greeks of the old stone age," and their art, which included drawings, engravings, paintings, and bas reliefs on cavern walls and floors and the carving of soapstone, bone, and ivory, shows a talent for line and form and is much better than that of the ancient Egyptians. It was clearly religious or magical in function. The art as well as the industry shows fluctuations; in particular, the art of flint working appears to decline with the increased use of bone for javelins and similar objects.

The Cro-Magnons were largely replaced during the slow and oscillating retreat of the fourth and last ice sheet by waves of other immigrants coming from the East. A curious instance of the presence of other and contemporary races is furnished by the two negroid skeletons found with Aurignacian implements in one of the caves of Grimaldi near Mentone on the Riviera. One is of a middle-aged female, the other of a boy of sixteen or seventeen years, both buried together and 2 feet below a layer with Cro-Magnon bones. They are short in stature and show many negroid characters in the skull, hip girdle, and limb proportions. They had low, flat faces with broad, flat noses, heavy jaws, large teeth, the incisors projecting.

No Grimaldi bones have been found anywhere else, but that this type was well known to the Cro-Magnons is suggested by some of their art. Various skeletal remains, notably from Brüx in Bohemia, and Brünn and Predmost in Moravia, have been cited as representatives of other races during Solutrean time.

The Cro-Magnons were followed by the so-called Grenelle-Furfooz races to which are referred a skull found at Grenelle, near Paris, in 1870, and 16 skeletons discovered at Furfooz, near Namur in Belgium, in 1867, representing a broad-headed race

that apparently invaded Europe up the valley of the Danube. These were contemporaneous with what is called the Azilian-Tardenoisian stage of culture, characterized by curious geometrically painted pebbles. They, possibly, were the progenitors of the modern Alpine race. Along the Baltic there is evidence of fishing races, possibly Teutonic.

These stages of human history as well as those which immediately follow, and which are shown in the time table, belong to anthropology and archeology rather than to paleontology, and were it not for their surpassing interest, this story would have concluded with the Neanderthalers and the appearance of the existing species of *Homo sapiens*.

The Robenhausian culture of the Swiss and other lake dwellings about 7000 B. C. shows permanent dwellings, boats, domestication of animals, and the cultivation of some crops, along with the use of pottery. Copper began to be used about 3000 B. C., the bronze age is estimated to have extended from about 4000 to 1800 B. C. in Asia and from 2000 to 1000 B. C. in Europe; the earlier iron age (Hallstatt) from about 1800 to 1000 B. C. in the Orient and from about 1000 to 500 B. C. in Europe.[1]

The problem of the prehistory of man is being actively attacked along many lines and new discoveries are constantly being made so that another generation will have solved many of the problems that still perplex us and will fill in the details, just as the archeological discoveries in Crete have substantiated what a former generation regarded as merely Homeric legends.

[1] These figures are from Obermaier.

GLOSSARY

A

Aboral.—The side of the body opposite to that on which the mouth is located.

Abstruse.—Difficult to be understood.

Abyssal.—The great deeps of the ocean, the organisms inhabiting them.

Aculeus.—The spined end of the sting in scorpions.

Aerial.—Adapted for flying.

Agnatha.—Lacking jaws.

Allantois.—Membranous, saclike appendage of the hinder alimentary tract found in the embryo of mammals, birds, and reptiles and serving to oxygenate the blood.

Ambulacrum.—One of the radial zones of plates in echinoderms, constituting food groove in the Pelmatozoa, associated with the underlying radial water, blood, and nerve systems. Name derived from the Latin and meaning a "covered way."

Amnion.—The membrane enclosing the embryo in mammals, birds, and reptiles.

Amphidetic.—The sort of ligament which extends both in front of and behind the beaks in certain bivalved mollusks.

Anapsidan.—Skulls lacking temporal fossæ.

Ancestrula.—The skeleton of the first zooid of a bryozoan colony.

Anisomyarian.—Bivalved mollusks with two unequal muscle scars on the interior of each valve.

Antennæ.—The second pair of sensory appendages in the Crustacea, the only pair in trilobites and insects.

Antennules.—The first pair of sensory appendages in the Crustacea.

Anthropology.—The study of man as an animal.

Anthropomorphic.—The ascribing of human characteristics to things which are not human.

Arboreal.—Dwelling in trees; adapted for life in trees.

Archæology.—The study of human antiquities.

Arcuate.—Curved.

Amphibious.—Adapted for living both in the water and on the land.

Aquatic.—Adapted for living in water.

Arenaceous.—Literally "sandy." Applied to Foraminifera which cement foreign particles together to form a shell.

Armlets.—See *Pinnules.*

Arthro.—Prefix from the Greek, meaning "jointed," *e.g.*, Arthrodira, "jointed neck;" Arthropoda, "jointed feet."

Arthrodira.—Extinct group of fishes with armor which is jointed at the neck.

Artifacts.—Fossil objects of artificial origin, as weapons or tools of chipped flint.

Atlas.—The first vertebra of the neck.

Atrium.—The central cavity of the sponge body.

Auricularia.—The early free-swimming stage of a sea cucumber (holothurian).

Autostylic.—Condition in lung fishes in which the first gill arch does not share in the jaw articulation.

Avicularia.—Certain zooecia in some Bryozoa which are modified to form an appendicular organ.

Axial.—In the median line. Applied especially to the central arched portion of the trilobite body.

Axis.—The same as axial. Specifically the second vertebra of the neck in mammals.

B

Benthonic.—Bottom-dwelling life.

Bilocular.—Two chambered, as in shells of some Foraminifera.

Biped.—Walking on two legs, as in man.

Bipinnaria.—The early free-swimming stage of a sea star.

Biramous.—Two branched.

Biserial.—In two series.

Bivalved.—With a shell of two pieces or valves, as in brachiopods, certain Crustacea, and the class Lamellibranchiata among the Mollusca.

Body Whorl.—The last-formed whorl of a gastropod shell.

Brachia.—The arms of a crinoid; the pair of appendages of a brachiopod.

Brachial.—A joint of a crinoid arm; the dorsal valve of a brachiopod shell.

Brachiation.—Swinging among the branches of trees by means of the arms and hands, as in monkeys and apes, especially the gibbons.

Brachidium.—The looped or spiral calcareous supports of the brachial appendages in the Telotrematous Brachiopoda.

Brachiole.—Small jointed appendages from the food grooves in the more primitive echinoderms (the Pelmatozoa).

Brachycephalic.—With short, broad skull.

Brachydont.—Low-crowned teeth.

Brachypodous.—Short-legged quadrupeds.

Branchia.—Gills.

Branchiata.—Arthropods breathing by means of gills, as in the Crustacea.

Brevicone.—A short cone.

Browsing.—The habit of many herbivorous animals of living largely on foliage stripped from the branches, a more ancient mammalian habit than grazing.

Bunodont.—Teeth with conical tubercles on the crown.

Byssus.—A horny secretion by which many bivalved mollusks are temporarily or permanently attached to some foreign object.

C

Callus.—An overlay of calcareous material in the gastropod shells, particularly on the inner side of the aperture.

Calyx.—The part of a crinoid crown containing the principal viscera, that is, the crown minus the arms.

Camerate.—Divided into chambers, as the shells of nautiloids and ammonoids. Also applied to an order of crinoids which had a solid dome.

Cannon Bone.—Compound bone formed by the coossification of two or more long bones of the foot.

Cardinal Area.—The area between the hinge and the beaks in certain Lamellibranchiata and Brachiopoda.

Carnassial.—Shearing or sectorial cheek teeth of the Carnivora.

Carnivorous.—Subsisting on animal food.

Carpus.—The bones of the wrist.

Cartilage.—Translucent, elastic, gristly tissue.

Cartilage Bone.—Bone ossified from cartilage.

Caudal Rami.—See *Cercopods.*

Cement.—The softer bony tissue entering into the composition of the teeth.

Centrum.—The body of a vertebra.

Cephalon.—The consolidated anterior part of a trilobite test.

Cephalothorax.—The consolidated head and thorax of many arthropods, as a lobster or crayfish.

Cerci.—Sensory appendages on the hind end of many insects.

Cercopods.—Sensory appendages on the hind end of many aquatic arthropods.

Cervical.—Of the neck; specifically, the cervical or neck vertebræ.

Chelæ.—Appendages with pincers, as in the lobster.

Chelate.—With pincers.

Chelicerœ.—The first pair of appendages in the Arachnida.

Chilaria.—The seventh pair of appendages in Limulus.

Chitin.—An amorphous horny substance, as finger nails, the skeleton of graptolites, etc.

Chitinous.—Consisting of chitin.

Conch.—Commonly applied to various gastropod and cephalopod shells; specifically, the main part of the shell as distinguished from the initial protoconch.

Conchyolin.—The organic compound forming the basis of molluscan shells.

Chondrophore.—A spoonlike calcareous projection in certain thin-shelled Lamellibranchiata in which the hinge has become obsolete and into which the resilium fits.

Cirri.—Jointed appendages on crinoid stems.

Clavicle.—The collar bone.

Cnidoblast.—A poison cell of the Cœlenterata.

Cœlomata.—Animals with a body cavity.

Cœlome.—The body cavity.

Cold Blooded.—Animals which lack means for changing their body temperature, that is, all animals except birds and mammals.

Columella.—The axis of a normal coiled gastropod shell.

Column.—The stalk in crinoids.

Columnal.—A joint of a crinoid stalk.

Compressed.—Squeezed or flattened in a vertical plane.

Condylarthra.—An extinct order of hoofed mammals.

Condyle.—An articular protuberance.

Convolute.—Gastropod shells in which the body whorl covers all of the earlier whorls.

Coracoid.—A curved bone, fused with the shoulder blade in the more specialized mammals.

Corona.—The calyx and arms of a crinoid; the main part of the test in echinoids.

Cranidium.—The central part of a trilobite cephalon consisting of the glabella and the fixed cheeks.

Cranium.—The part of the skull above and behind the eyes, which lodges the brain.

Crest.—Term applied to any convexity of the margin of the aperture of a cephalopod shell.

Cro-Magnon.—An extinct race of stone-age men in western Europe belonging to the species *Homo sapiens,* distinguished for their cave art.

Crown.—See *Corona.*

Crura.—The calcareous outgrowths from the front of the hinge plate in the dorsal valve of brachiopods.

Cruralium.—Applied to platelike crura which become united, as in the Pentamerus Brachiopoda.

Ctenidia.—The gills of the Mollusca.

Cursorial.—Adapted for running, as the horse.

Cyrtocone.—A curved cephalopod shell.

Cystiphragm.—Name applied to the partitions in the zooecia of many bryozoa.

D

Delthyrium.—The pedicle opening in the brachiopod shell.

Deltidial Plates.—A pair of plates in the Telotrematous Brachiopoda partially closing the delthyrium.

Deltidium.—The plate in the Protrematous Brachiopoda partially closing the delthyrium.

Dendroid.—Treelike.

Dentary.—The lower jawbone in mammals.

Dentine.—Tooth tissue which is harder than cement but less hard and dense than enamel.

Depressed.—Squeezed or flattened in a horizontal plane.

Dermal.—Pertaining to the integument, such as scales and spines in fishes, feathers in birds, hair and nails in mammals.

Dextral.—Gastropod shells coiled from left to right.

Diaphragm.—A name applied to partitions in the zooecia of many bryozoa; a general term for partitions; the muscular partition separating the thorax and abdomen.

Diapsidan.—Having two pairs of temporal fossæ in the skull.

Dibranchiate.—With two gills, as the squid.

Digit.—A finger or toe.

Digitigrade.—Walking on the digits, as in a cat or dog.

Dimorphism.—Species with two body forms, as among the Hydrozoa.

Dimyarian.—Lamellibranchiata with two adductor muscle scars on the interior of each valve.

Dipleurula.—The hypothetical ancestor of the Echinoderma.

Diplopores.—The paired pores in the plates of certain cystoids.

Dissepiments.—Unoriented calcareous filling of the older and no longer occupied part of a coral skeleton.

Distad.—The direction away from the point of attachment.

Distal.—Most distant from the point of attachment.

Distichous.—Arranged in two opposite parallel rows.

Dolichocephalic.—With an elongated skull.

Dorsal Vertebræ.—Those which carry the ribs.

Doublure.—The inflected or incurved border of the trilobite test.

Dynamic.—Active, as opposed to "static," organisms.

E

Ecdysis.—The moulting of the exoskeleton, as in crabs.

Ectoderm.—The original outer body layer.

Embryo.—The unborn or prenatal stage of an animal, often called the "fetus" in vertebrates.

Enamel.—The dense and very hard calcareous tissue entering into the construction of the teeth and certain fish scales.

Endocones.—More or less conical, horny, epidermal secretions left in the chambers of cephalopod shells.

Endocyclic (Regular).—Applied to echinoid tests which are radially symmetrical.

Endoderm.—The original inner body layer.

Endogastric.—Cephalopod shells coiled toward instead of away from the venter, oppositely from the normal exogastric coiling.

Endopodite.—The inner branch of a crustacean or trilobite appendage.

Escutcheon.—An area behind the beaks in certain lamellibranchs which is marked differently from the rest of the outer surface of the shells.

Exocyclic (Irregular).—Applied to those echinoids in which the test is bilaterally symmetrical.

Exogastric.—Cephalopod shells coiled away from the venter, the normal coiling.

F

Facial Suture.—Applied particularly to the line of juncture between the free cheeks and cranidium in trilobites.

Femur.—The thigh bone, or upper leg bone.

Feral.—Wild animals descended from domesticated ancestors.

Fibula.—The outside lower leg bone.

Foramen.—Perforation of a hard part, especially of bones for the passage of a nerve or blood vessel. One of the punctures in the test of the punctate Foraminifera.

Foramen Magnum.—The opening in the base of the skull through which the spinal cord joins the brain.

Fossæ.—Pits or depressions in bones, as the temporal fossæ or vacuities on the sides of the skull.

Fossorial.—Animals which burrow, applied especially to terrestrial vertebrates with such habits.

Frugivorous.—Subsisting on a diet of fruits (including nuts and seeds), as do the apes.

Funnel.—A term frequently applied to the swimming organ of the cephalopods, also to the calcareous flanges of the siphuncle.

Fusiform.—Shaped like a spindle.

G

Genal.—The angle or spine where the lateral and posterior margins of a trilobite cephalon meet.

Genital.—Pertaining to reproduction, particularly the interradial and usually perforated plates of the apical system of echinoids.

Genus.—One or more closely related species.

Gibbous.—With an inflated form.

Girdle.—The flexible band which holds the shell pieces together in the molluscan class Amphineura.

Glabella.—The elevated axial region of the trilobite cephalon.

Glenoid.—Articular surface on the squamosal for the lower jaw; articular socket on the scapula for the head of the humerus.

Glissant.—Animals which glide through the air but lack true flight, as the so-called "flying squirrels."

Gnathobase.—Basal joints of the appendages around the mouth modified for crushing food in many arthropods.

Gonad.—A reproductive gland.

Gonangium.—The cavity in certain Hydrozoa and graptolites in which new individuals are developed. Also called Gonotheca.

Goniatites.—Ancestral ammonites with angular sutures.

Gonotheca.—See *Gonangium.*

Grazing.—Cropping grass or other vegetation from the ground.

Gregarious.—Animals which live in herds or flocks.

Guard.—The hinder part of the vestigial shell in the belemnites.

Gyracone.—A partially and loosely coiled cephalopod shell in which the whorls are not in contact.

H

Hæmal.—The visceral side of the body, dorsal in invertebrates, ventral in vertebrates.

Hallux.—The first digit of the foot; the great toe.

Herbivorous.—Subsisting on vegetable food.

Heterodont.—Diversely modified teeth.

Heteromyarian.—Lamellibranchs with two unequal adductor muscle scars on the inner side of each valve.

Hexagonal.—Six sided.

Homodont.—With teeth all essentially alike.

Homœdeltidium.—The plate in Atrematous and Neotrematous Brachiopoda corresponding to the deltidium, which see.

Humerus.—The upper arm bone.

Hydropore.—A perforated plate near the mouth in some crinoids.

Hydrospires.—The folds in the plates at the sides or beneath the ambulacra in certain echinoderms, especially in the Blastoidea.

Hyponomic Funnel.—The muscular tubular organ which conducts water in and out of the mantle cavity of the cephalopods in respiration, and which by violently ejecting water enables the animal to swim backward.

Hypostoma.—The chitinized plate in front of the mouth on the underside of the trilobite cephalon.

Hypsodont.—High-crowned cheek teeth.

I

Ilium.—The uppermost of the three pelvic bones, distinct in reptiles and birds, coossified with the ischium and pubis in mammals.

Imago.—The adult stage in insects.

Innominate Bone.—The compound bone forming the right and left halves of the pelvis in mammals, made up of the consolidated ilium, ischium, and pubis.

Interambulacral.—Plates or other structures located interradially, that is, between the ambulacral areas, in the Echinoderma.

Involute.—Shells that are very tightly coiled.

Ischium.—The hinder of the three pelvic bones, distinct in the reptiles and birds, consolidated with the ilium and pubis in mammals.

Isomyarian.—Lamellibranchs with two equal adductor muscle scars on the interior of each valve.

J

Jugum.—A calcareous bar connecting the spiralia in the brachiopod superfamily *Spiriferacea.*

L

Lappets.—Prominent lateral crests of the aperture of some ammonite shells.

Larva.—Usually, the first free stage in the ontogeny of animals where they differ from the adults; particularly, that stage in the insects.

Ligament.—A band of fibrous tissue uniting bones or forming joints; in the bivalved mollusks an elastic tissue for opening the valves of the shell.

Limb Girdles.—The bones to which the limbs are attached in vertebrates.

Lobes.—Depressions away from the aperture on the septa of ammonites.

Lophophore.—The lunate or circular row of tentacles in the Bryozoa; the pair or single brachial appendage in the Brachiopoda.

Lunate.—Crescent shaped.

Lunule.—An area in front of the beaks in certain lamellibranchs differently marked from the balance of the outer surface of the shells.

M

Madreporite.—The perforated area in sea stars and sea urchins which admits water into the water-vascular system.

Mamelon.—The articular protuberance of the larger tubercles on the test of a sea urchin.

Mandible.—The lower jaw in mammals.

Mantle.—The outer surface of the molluscan body which secretes the shell.

Manus.—The hand, or forefoot in quadrupeds.

Maxillary.—The upper jawbone.

Mega.—Prefix from the Greek, meaning "large."

Megalosphere.—See *Megasphere*.

Megasphere.—The asexual generation in Foraminifera which has large initial chambers.

Mesoderm.—The original middle body layer.

Mesosoma.—The region behind the Prosoma in scorpions and merostomes, normally of six tergal segments.

Metacarpus.—The long bones of the hand.

Metasoma.—The terminal completely ringed segments of the scorpion body, normally of six rings, also applied to the Merostomata.

Metastoma.—A small chitinized plate behind the mouth in some trilobites.

Metatarsus.—The long bones of the foot.

Micro.—Prefix from the Greek, meaning "small."

Microphagous.—Subsisting on microscopic food.

Microsphere.—The sexual generation in Foraminifera which has small initial chambers.

Miliary.—The smallest grade of tubercles on the tests of echinoids.

Monomyarian.—Lamellibranchs with a single adductor muscle scar on the interior of each valve.

Monophyletic.—Descendants of a single ancestral type.

Monothalmous.—Single chambered, applied particularly to tests of Foraminifera.

Morphological.—Having to do with form in organisms.

Myophore.—Calcareous internal process projecting from beneath the beaks to support the viscera in pholad shells.

N

Nasals.—A pair of bones forming the roof of the nasal passage.

Natatorial.—Adaptations for a swimming life.

Nauplius.—The first free-swimming stage in many Crustacea.

Nautilocone.—A cephalopod shell in which the last whorl conceals all of the earlier whorls.

Neck Furrow.—See *Occipital Furrow*.

Nectonic.—Actively swimming aquatic animals.

Nema.—The threadlike process of attachment of the first individual of a graptolite colony.

Nemacaulis.—The axis of a graptolite stock; the equivalent of the hydrocaulis of a modern hydrozoan.

Neural (Nervous).—The side of the body occupied by the main nervous trunk, dorsal in vertebrates, ventral in invertebrates.

Nocturnal.—Animals that are active at night and rest in the daytime.

Nodals.—The larger joints arranged at intervals on crinoid stems.

Notochord.—An elastic, rodlike axial structure beneath the neural trunk in the simpler Chordata.

Nucleus.—A term sometimes applied to the earlier part of gastropod shells which is distinguished from the adult condition by differences in color, texture, or ornamentation.

Nummulites.—Discoid many-chambered foraminifera with planospiral tests.

Nummuloidal.—Shaped like a pile of coins.

O

Occipital Condyle.—Protuberance from the occiput for articulation with the first vertebra, single in birds and reptiles, paired in amphibians and mammals.

Occipital Furrow.—The last furrow of the glabella in trilobites.

Occiput.—The posterior part of the skull.

Ocelli.—Simple eyes or eyespots.

Ocular.—The radial plates of the apical system in echinoids, situated at the aboral end of the ambulacral systems.

Œcium—The walls of a bryozoan polypide.

Omnivorous.—Subsisting upon all kinds of food.

Ontogeny.—The life history of an individual.

Operculum.—A lid.

Ophiocone.—A cephalopod shell coiled like a length of rope, with all of the whorls visible from the side.

Opisthodetic.—Bivalved mollusks in which the ligament is located behind the beaks.

Opisthoparian.—Trilobites in which the hinder part of the facial sutures cuts the margin of the cephalon behind the genal angle.

Oral.—That surface of the body on the same side as the mouth; certain plates around the mouth in the Pelmatozoa.

Orbit.—The bony socket of the eye.

Orbitoids.—Diskoid foraminifera with many chambers arranged in rings or cycles.

Orthocone.—A straight (not coiled) cephalopod shell.

Ostracoderm.—Literally, "bony skinned," a group of extinct fishes with an armor of bony plates.

Ovicell.—Cavity in which the eggs of certain Bryozoa are incubated.

Oviparous.—Egg-laying animals.

Ovipositor.—An abdominal appendage in insects for the deposition of the eggs.

P

Palate.—The bony roof of the mouth.

Pallial Line.—Thin groove on the inside of the shell in many lamellibranchs marking the attachment of the mantle muscles.

Pallial Sinus.—A loop or sinus near the hinder end of the pallial line in certain lamellibranch shells marking the attachment of the retractor muscles of the siphons.

Pallium.—The mantle of the Mollusca.

Palpebral.—The lobe or elevation on the margin of the fixed cheeks in trilobites, immediately inside the eye.

Palustrine.—Living in a swampy or marshy environment.

Papulæ.—Soft extensions through the pores in the tests of echinoderms for purposes of respiration.

Parapodia.—The paired appendages of the annelid worms.

Parapsidan.—Skulls of reptiles in which the single pair of temporal fossæ are above the postorbital and squamosal bones.

Pecora.—The true ruminants.

Pecten.—Comblike appendages of the second segment of the Mesosoma in scorpions.

Pedicle.—The stalk by which many brachiopods are attached.

Pedipalps.—The second pair of appendages in the Arachnida.

Peduncle.—Literally, "a stalk;" See *Pedicle.*

Pelvis.—The hip bones or girdle for the hind limbs.

Pen.—The internal vestige of the shell in the squids.

Pentagonal.—Five sided.

Peri.—Prefix from the Greek meaning "around."

Perignathic Girdle.—The thickened basal or peristomial margin of the corona in many echinoids.

Periproct.—The region around the anus in echinoids.

Peristome.—The region around the mouth in echinoids; the border of the shell aperture in gastropods.

Pes.—The foot.

Petal.—An echinoid ambulacral area with convex outlines like a petal of a flower.

Phalanges.—Plural form of phalanx.

Phalanx.—A finger or toe joint.

Phragmocone.—The septate part of the internal shell in the belemnoids.

Phylogeny.—Ancestral or racial history.

Phylum.—One of the major subdivisions of animals or plants the members of which are supposed to have been derived from a common ancestral type; also, used, especially by vertebrate paleontologists, for a single line of descent as distinguished from collateral lines.

Physiology.—The study of functions in organisms.

Pinnate.—Arranged like a feather. From the Latin *pinna*, a "feather;" applied particularly to such an arrangement of the pinnules on the arms of many crinoids.

Pinnules.—The side branches or armlets of a crinoid arm.

Placenta.—Organ by which the embryo is attached to the wall of the uterus in monodelphian mammals.

Planktonic.—Drifting or feebly swimming aquatic organisms in contrast to swimming or bottom-dwelling life.

Planospiral.—Coiled in a single plane.

Plantigrade.—Walking on the soles of the feet.

Planula.—The early free-swimming stage of a cœlenterate.

Plastron.—The ventral shell of a turtle. The differentiated plates on the oral side of certain irregular echinoids between the peristome and the periproct.

Pleuræ.—The lateral parts of the thoracic segments in trilobites.

Pleural.—The lateral body regions on either side of the axis in trilobites.

Pleurite.—Lateral units of the arthropod exoskeleton.

Plicate.—Folded, or ornamented with folds.

Pluteus.—The early free-swimming stage of a sea urchin, or echinoid.

Podia.—Greek for "feet;" often used as a suffix in scientific terminology; applied particularly to the tube feet of echinoderms.

Pollex.—The first digit of the hand; the thumb.

Polygonal.—Many sided.

Polymorphism.—Species with several body forms, as the different polyps of a hydrozoan colony.

Polyp.—The individual in the Cœlenterata and Bryozoa.

Polypide.—A single individual of a bryozoan colony.

Polyphyletic.—Of diverse ancestry.

Polyserial.—In many rows.

Polythalmous.—Many chambered; applied particularly to the tests in the Foraminifera.

Porcelaneous.—With a luster like porcelain; applied particularly to the tests of the imperforate calcareous Foraminifera.

Pore Rhombs.—Areas of tangential pores in certain cystoids.

Postabdomen.—See *Metasoma.*

Préabdomen.—See *Mesosoma.*

Predaceous.—Subsisting by preying on other animals; predatory; carnivorous.

Prenuncial.—Foreshadowing or presaging a later form or structure.

Prognathous.—With projecting jaws.

Proloculum.—The first or initial chamber of a foraminiferal test.

Proostracum.—A shelflike forward projection from the border of the phragmocone in the belemnoids.

Proparian.—Trilobites in which the hinder part of the facial sutures cuts the margin of the cephalon in front of the genal angle.

Prosoma.—The cephalothorax in scorpions and merostomes.

Protaspis.—The first free-swimming stage in trilobites.

Protegulum.—The first attached shelled stage in the development of a brachiopod.

Protoconch.—The first stage of the shell in gastropods and cephalopods, horny in nautiloids, calcareous in ammonoids and gastropods.

Protozoa.—Single-celled animals.

Proximad.—In the direction of the point of attachment.

Proximal.—Next the point of attachment.

Pseudopodia.—Protoplasmic extensions from the surface of a protozoan.

Pubis.—One of the three pelvic bones, distinct in reptiles and birds, coossified with the ilium and ischium in mammals.

Pupa.—The inactive stage intervening between the larval and adult stages in many insects.

Pygidium.—The consolidated posterior region of a trilobite.

Pygostyle.—The plowshare bone at the end of the vertebral column in modern birds, made up of consolidated caudal vertebræ.

Q

Quadrangular.—Four sided.

Quadrate.—A bone between the lower jaw and the skull in most vertebrates other than mammals, represented by the malleus or incus of the mammalian ear.

Quadruped.—A four-limbed animal.

R

Radius.—The inner bone of the lower arm.

Radula.—The cartilaginous extension from the buccal cavity in mollusks (except lamellibranchs, in which it has been lost) beset with tiny chitinous teeth, often called the "tongue."

Ramules.—See *Pinnules.*

Rectrices.—Tail feathers in birds.

Reniform.—Kidney shaped.

Resilifer.—The depression on the hinge plate of a bivalved mollusk in which the resilium fits.

Resilium.—An internal elastic ligament which serves to open the valves by compressional elasticity in many bivalved mollusks.

Rhabdosome.—A single stock of a graptolite colony.

Rhombic or **Rhomboidal.**—A four-sided form with two opposite angles obtuse and two acute.

Rostrum.—The crest on the ventral margin of the shell aperture in ammonites; the hinder reinforced part of the vestigial shell in belemnoids.

Ruminant.—Applied to animals which chew the cud; cattle.

S

Sacrum.—The fused vertebræ for support of the pelvis and hip bones.

Saddles.—Elevations on ammonite septa toward the aperture.

Sagittal Crest.—A median ridge of bone on the roof of the skull.

Saltatorial.—Adaptations for jumping; jumping animals, as the kangaroo.

Scansorial.—Animals with a climbing habit, as a squirrel.

Scapula.—The shoulder blade.

Scleroblast.—The spicule secreting cells in the sponges.

Scrobicule.—The smooth ring around the mamelon of an echinoid tubercle.

Sculling.—Propulsion, as in fishes, by the side-to-side motion of the hind end.

Selenodont.—Teeth with lunate cusps.

Septa.—The vertical radial plates in a coral skeleton; the partitions etween the chambers in a cephalopod shell.

Septate.—Divided into chambers, as in nautiloid and ammonoid shells.

Septulæ.—Communicating pores in the walls of Bryozoa.

Setose.—Beset with setae or bristles.

Shoulder Girdle.—The bones to which the forelimbs are attached.

Sicula.—The first individual of a graptolite colony.

Sinistral.—Gastropod shells coiled from right to left, oppositely from the normal dextral coiling.

Sinus.—Applied to any concavity along the margin of the aperture of a cephalopod shell.

Siphon.—The extended and united posterior mantle edges in lamellibranchs and gastropods for providing inhalent and exhalent water currents; the modified hinder foot in the cephalopods through which the water is ejected in breathing and swimming: the fleshy cord extending backward from the body through the siphuncles in the cephalopods.

Siphuncle.—The hole and associated hard parts in the septa of shelled cephalopods occupied by a fleshy backward prolongation from the body.

Spicule.—Small calcareous or siliceous bodies or skeletal elements in the tissues of invertebrates, especially the sponges and cœlenterates.

Spiracles.—The exits of the hydrospires around the mouth in the blastoids.

Spiralia.—Applied to the spirally coiled brachidia in the superfamily Spiriferacea of the Brachiopoda.

Spire.—The whorls of a gastropod shell above the body whorl.

Spondylium.—A ventral platform for muscle attachment in the lower valve of many brachiopods.

Static.—Without motion, the opposite of "dynamic."

Sternal Ribs.—The lower segments of the ribs which articulate with the sternum.

Sternite.—Ventral segments of the exoskeleton of arthropods.

Sternum.—The breastbone in vertebrates.

Stigmata.—The external openings of the tracheæ in non-aquatic arthropods.

Suture.—The line of juncture between parts, as in the cranial bones of a vertebrate or between the outer walls of chambers or whorls of a shell of a foraminifer or mollusk; particularly applied to the junction between the shell walls and the septa in cephalopods.

Symphysis.—Coossification, particularly the line of union of the two halves of the lower jaw in mammals.

Synapsidan.—Skulls of reptiles in which the single pair of temporal fossæ are below the postorbital and squamosal bones.

Synapticulæ.—Tangential bars between the septa in a coral skeleton.

T

Tabulæ.—Cross-partitions in the coralla of many Anthozoa.

Tabulium.—Name frequently applied to partitions in the zooecia of many Bryozoa.

Tarsus.—The bones of the ankle.

Taxodont.—A type of hinge structure in certain bivalve mollusks in which there are numerous subequal teeth.

Teeth.—Structures or processes for the prehension and mastication of food; interlocking processes for fixing and guiding the valves of the shell, as in the Lamellibranchiata.

Tegmen.—The area enclosed by the arms in the crinoids.

Teleodont.—A type of hinge structure in lamellibranchs in which there are a few well-developed cardinals centrally located, with or without long, platelike laterals.

Telson.—The terminal plate or spine in many aquatic arthropods, as in the horseshoe crab, Limulus.

Tendon.—A tough connective between muscle and bone; a sinew.

Tergites.—Dorsal parts of the exoskeleton of arthropods.

Terrestrial.—Adapted for life on the land.

Test.—A general term applied to the exoskeleton of many invertebrates.

Tetrabranchiate.—With four gills, as in the pearly nautilus.

Tetraserial.—In four series.

Theca.—The wall of a coral skeleton; the cup or denticle which houses the individual in a graptolite colony.

Tibia.—The inner bone of the lower leg; the shin bone.

Tornaria.—The swimming larval stage of Balanoglossus—one of the primitive Chordata.

Tracheata.—Arthropods breathing by means of ramifying air tubes, as in the insects.

Trochosphere.—The aquatic free-swimming early stage of a mollusk.

Truncate.—Abruptly cut off.

Turbinate.—Top shaped.

U

Ulna.—The outer bone of the lower arm.

Umbilicus.—The navel in placental mammals; more particularly, the channel along the axis of those gastropod shells where the inner parts of the whorls do not fuse to form a columella; the depressions on the two sides of the axis in a cephalopod shell.

Ungual Phalanx.—The distal joint of a digit which carries the claw, nail or hoof.

Unguiculate.—Having claws on the toes, particularly in mammals.

Unguligrade.—Walking on the ends of one or more digits, as in the specialized ungulates.

Uniserial.—In a single series.

Univalved.—Mollusks with a shell in one piece, as in a snail or a nautilus.

V

Vacuities.—Applied to spaces in the skull unoccupied by bone; fossæ.

Valves.—The right and left shells of lamellibranchs or dorsal and ventral shells of a brachiopod.

Venter.—The ventral region of a cephalopod shell.

Vermiform Appendix.—A slender diverticulum of the cæcum in man and apes.

Vertebra.—One of the joints of the backbone.

Vesicular.—Full of cavities, spongy.

Vestigial.—Traces of a once functional part.

Vibracula.—Flexible bristle-like appendages in certain Bryozoa.

Virgula.—The stiffening rod in the wall of a graptolite stock.
Vitreous.—Glassy.
Viviparous.—Born alive.
Volant.—Able to fly.

W

Warm Blooded.—Animals which can change their body temperature (mammals and birds).
Whorl.—Once around an axis of coiling, as in a snail shell or foraminiferal test.

Z

Zooecium (plural Zooecia).—The wall of a bryozoan polypide.
Zooid.—The single individual of a colony, especially in the Cœlenterata; a polyp.
Zygomatic Arch.—A bridge of bone from the eye socket to the hinder part of the cranium.

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